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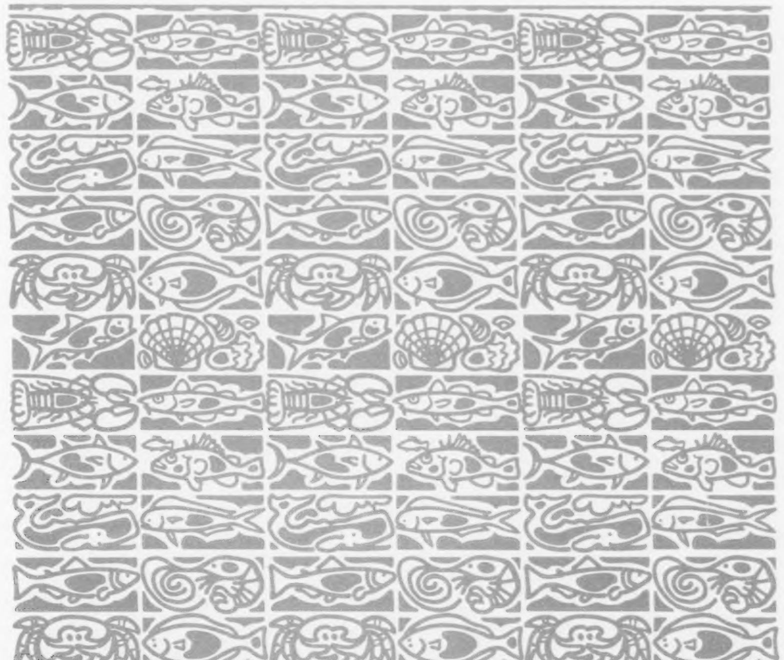

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Abstract.–Because of their tendency to return to natal streams, salmonid populations have often been viewed in ecological isolation, although the notion of an evolutionarily significant unit (ESU) recognizes dispersal on evolutionary time scales. We investigated the consequences of dispersal (straying) on an ecological time scale where straying creates a metapopulation structure for salmonid streams within an ESU. We developed a simple model for salmonid metapopulations, focusing on source and sink populations, and used the model to highlight the dangers of ignoring this structure in conservation efforts. We show that exactly the wrong conservation efforts may occur if metapopulation structure exists but is ignored.

The dangers of ignoring metapopulation structure for the conservation of salmonids

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The U.S. National Marine Fisheries Service (NMFS) Status Review of Coho Salmon (*Oncorhynchus kisutch*) from Washington, Oregon, and California (Weitkamp et al., 1995) formalized the agency's approach to defining both the boundaries and conservation status of distinct segments of salmonid populations for potential listing under the Endangered Species Act. With this approach, originally developed by Waples (1991), a population or group of populations is considered distinct if they are ". . . substantially reproductively isolated from conspecific populations," and if they are considered ". . . an important component of the evolutionary legacy of the species" (Weitkamp et al., 1995, p. 3). A distinct population or group populations is referred to as an evolutionarily significant unit (ESU) of the species.

For a group of populations to be classified as an ESU, the populations must be reproductively isolated from other populations but not from each other. An ESU also implies successful dispersal and reproduction between populations on an evolutionary time scale. A metapopulation is a group of populations (demes) linked by dispersal of individuals on a shorter ecological time scale such that dispersal affects both the genetics of the individual demes and their abundance and dynamics (Levins, 1969; Ruxton, 1996; Ruxton and Doebeli, 1996). To maintain consistency with the ecological literature, we have used the term "metapopulation" to refer to the group of populations or demes, and the term "population" or "deme" (often used interchangeably, see Policansky and Magnuson, 1998) to refer to one of the individual populations that make up the metapopulation. ESUs and metapopulations overlap on the continuum of population structures. Although a metapopulation will always compose part of, or the entire, ESU, an ESU does not have to contain any metapopulation structure. Dispersal between demes within a metapopulation must be great enough to affect the dynamics of the demes and the recolonization of habitats of extinct demes. Within an ESU, dispersal must only be great enough to contribute to the genetic make-up of component populations; it does not have to lead to recolonization events or affect the population dynamics.

Salmon typically return to their natal streams to spawn. However,

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some individuals stray to streams other than their natal one, and those streams may be inhabited or uninhabited by other conspecifc populations (Ricker, 1972; Quinn, 1993). Indeed, straying constitutes the process by which salmonids colonize new habitats (Milner and Bailey, 1989; Wood, 1995). Individuals that stray during the spawning migration may thus serve as the mechanism for dispersal between salmonid populations on both an evolutionary and ecological time scale.

Reliable estimates of the magnitude of straying are rare and span a wide range of values across and within species (Quinn, 1993; Pascual and Quinn, 1994). Quinn and Fresh (1984) documented a straying rate of 1.4% in their study of wild chinook salmon (*Oncorhynchus tshawytscha*) from the Cowlitz River Hatchery, Washington. Quinn et. al (1991) estimated hatchery straying rates ranging from 9.9 to 27.5% for five populations of autumn chinook on the Columbia River. Heard (1991) estimated that, in general, nearly 10% of wild pink salmon (*Oncorhynchus gorbuscha*) stray from their natal streams. Labelle (1992) estimated that approximately 4.7% of individual coho salmon strayed between nine separate streams along the coast of Vancouver Island, British Colombia, but that straying could be greater than 40% for some streams in some years. Genetic studies such as that of Gall et al. (1992) suggest that the average number of migrants exchanging genes per generation (Nm) in west coast Chinook salmon populations is on the order of 5–15 individuals.

Because the incidence of straying is common and the magnitude of straying is so variable, it is quite likely that metapopulation structure could exist for at least some salmonid populations. In fact, the National Research Council's report on Pacific Northwest salmonids recognizes that "... maintaining a metapopulation structure with good geographic distribution should be a top management priority to sustain salmon populations over the long term" (NRC, 1996, p. 8). Given the geographic scale of the straying documented in the previous studies, compared with the range of an ESU (note that the entire West Coast comprised only six ESUs), it is possible that a single ESU may even contain multiple metapopulations, as would be expected because ESUs are explicitly evolutionary constructs, whereas metapopulations are explicitly ecological constructs.

In this paper, we investigate the implications of metapopulation structure for conservation efforts given a variety of spatial scales. In particular, we identify the problems such structure could cause for managers if it left undetected. If one is concerned strictly with the risk of extinction for a species, metapopulation structure may be quite beneficial (Levins, 1970; Hanski and Gilpin, 1991; Hanski, 1994; Ruxton, 1996; Ruxton and Doebeli, 1996). Because the metapopulation occurs in patches (each of which contains a deme with its own probability of extinction) and because these demes are connected through dispersal, if any single deme becomes extinct, then there is a nonzero probability that the patch will be recolonized by individuals from another deme. Over time, an individual patch may therefore experience multiple extinctions and recolonization events. These events result in the metapopulation as a whole persisting far longer than any one of its individual demes. Potential problems arise when one is concerned not just with the risk of extinction but with the management (and therefore monitoring) of these populations.

In the most simple metapopulation model, one assumes that all demes, and the patches they inhabit, are identical (Levins, 1970). This, however, need not be the case, and in the real world, is likely not to be the case. One metapopulation model that takes such variation into account is the source-sink metapopulation model (Pulliam, 1988). In this model, sink habitats are patches where local mortality exceeds local reproduction (so that $R_0<1$ or $r<0$). In other words, without individuals immigrating to the patch, a sink population cannot sustain itself. Source patches, on the other hand, are patches where local reproduction exceeds the sum of local mortality and emigration (so that $R_0>1$ or $r>0$). Populations in source habitats can persist without the populations in the sink habitats, but the opposite is not true. There are no assumptions regarding the relative abundance of individuals between these source and sink patches. In fact, it is quite possible for the sink patches to have larger populations than source populations (Pulliam, 1988). For example, if competitively dominant individuals hold territories of fixed size (as is the case with some bird species), a source habitat would be highly productive, yet would have a constant population size because all subdominant individuals would be forced to disperse. If this dispersal rate into the sink habitats were greater than the natural rate of decline (the difference between births and deaths) in the sinks, then sink habitats could contain more individuals than the source habitats. In such a case, undetected metapopulation structure could lead managers astray.

When metapopulation structure (especially source-sink dynamics) exists, the abundance of a species in an area can be disconnected from the specific survivorship and fecundity rates of that area owing to the effects of immigration. If ignored, this disconnection poses two problems for managers, both of which are made worse if the jurisdiction of the manager does not cover the complete metapopulation. First, if managers are looking strictly at the abundance of individuals, they could be lulled into a false sense of security. The size of the demes in the source and sink habitats could be relatively constant despite the fact that, without the demes in the source, the demes in the sink would become extinct. Brawn and Robinson (1996) uncovered this very scenario with Neotropical migrant birds in Illinois.

The second problem is even more insidious. If deme abundance is no longer a good indicator of habitat quality, managers could be led into conserving the wrong type of habitat (van Horne, 1983; Pulliam, 1988). Gowan and Fausch (1996) demonstrated how this could occur regarding the effects of habitat changes on the demography of a variety of trout species in Colorado, although they did not discuss their results in terms of metapopulations. Over an eight-year period (four generations of trout), Gowan and Fausch (1996) discovered that the addition of woody debris in treatment areas significantly increased the number of individuals and the total trout biomass in treatment areas in relation to the control areas. However, with the aid of fin marks (clipped fins) and individual tags, they discovered that survival, individual growth, and recruitment rates in the treatment areas were not significantly different from those in the control areas. Immigration from outside the study area to the treatment sites was solely responsible for the increase in abundance and total biomass. If Gowan and Fausch (1996) had not been able to account for immigration to the site, they would likely not have been able to discern the true effects of the addition of woody debris and would have likely mistaken increased density for increased habitat productivity (cf. Hunter, 1991). Although source-sink metapopulation structure was not the cause of these results, such an example demonstrates how reliance on abundance or density estimates can lead managers astray when immigration or emigration is not taken into consideration.

Those faced with the responsibility of managing salmonid populations may encounter these very problems and issues. In the remainder of this paper, we develop a model to help focus ideas about the potential dangers of undetected metapopulation structure for salmonid conservation.

Materials and methods

The model

The model is simple, and the form of the model was chosen for ease of comprehension. We found that even such a simple model was adequate to illustrate the possible consequences of ignoring metapopulation structure.

We considered a group of generic salmonid demes that reside in streams that are distributed evenly along some waterway but that are close enough so that straying between any of the two groups is possible (though not necessarily with equal probability). The scale was completely generic. The streams could be tributaries to a single river, rivers within a watershed, or even separate watersheds. Next, we numbered these streams consecutively along this waterway. Each deme was then indexed by the number associated with the stream in which it resides (e.g. deme 4 resides between deme 3 and deme 5 along this waterway). For computational purposes, we considered 10 streams, which is equivalent to a metapopulation consisting of 10 demes spread over 10 patches. Assuming that density-dependent effects could be ignored (which, except for Allee effects, would be the case for any recovering population), the fundamental variables are

$N(i,t)$ = the deme abundance in stream i in year t;
$r(i,t)$ = the per-capita reproduction in stream i in year t;
$s(j,i,t)$ = the number of fish that stray from their natal stream j to stream i in year t; and
f = the fraction of fish that stray from their natal stream (assumed equal for all demes).

For simplicity's sake, we assumed that strays have the same reproductive potential as nonstrays in a given stream. This assumption decreases the parameter space but does not affect overall dynamics of the model. It does, however, limit the direct applicability of our specific examples to streams that are relatively close in proximity, yet, as will be explained, does not diminish the danger for management at the watershed, basin, or even ESU level. By incorporating an additional parameter to account for the differential reproductive potential, some of the dynamics would simply have been dampened, making them more difficult to perceive. Therefore, the population dynamics for a deme are

$$N(i,t+1) = r(i,t)\left\{N(i,t)(1-f) + \sum_{j \neq i} s(j,i,t)\right\}. \qquad (1)$$

As with differential reproduction, the assumption that there are more complicated population dynamics (e.g. Ricker stock-recruitment relationships) would not change the basic message of our paper but would make it harder to perceive. In a more complicated model, or one designed for a nongeneric salmonid, the model would be indexed by generation time instead of year, but the potential problems described in this paper would still apply.

We assumed $s(j,i,t)$ is an exponential function of the distance between stream i and j (see Hanski, 1994). We assumed that the streams are evenly spaced along the waterway and numbered consecutively, so that the distance between stream i and stream j is proportional to $|i-j|$. Therefore, the number of individuals straying from stream j to stream i is

$$s(j,i,t)=\frac{N(j,t)fe^{-m|i-j|}}{\sum\limits_{k\neq j} e^{-m|k-j|}} \qquad (2)$$

where m defines the rate at which straying decreases with distance, and the denominator is a normalization so that all strays end up in a stream (i.e. none are lost to the system).

We assumed that per-capita reproduction rate of each deme is a function of some baseline rate of per-capita reproduction that is equal for all streams (e.g. ocean conditions and harvest) plus a function of a component of the habitat that contributes positively towards per-capita reproduction (e.g. width of the riparian zone) and a function of a component of the habitat that contributes negatively to per-capita reproduction (e.g. road density). If z_0 is the baseline per-capita rate of reproduction and $z_1(i,t)$ and $z_2(i,t)$ are the amounts of the beneficial and detrimental habitat components for stream i in year t, then the per-capita rate of reproduction for stream i in year t is modeled as

$$r(i,t)=z_0+g\left\{1-e^{-z_1(i,t)}\right\}-b\left\{1-e^{-z_2(i,t)}\right\} \qquad (3)$$

where g = the maximum increase in the per-capita reproduction due to the beneficial habitat component; and
b = the maximum decrease in the per-capita reproduction due to the detrimental habitat component.

As $z_1(i,t)$ increases, $e^{-z1(i,t)} \to 0$, so that the effect of the beneficial habitat component approaches an asymptote at g. Similarly, the detrimental habitat component approaches an asymptote at b. Therefore, $r(i,t)$ is constrained to lie between z_0-b and z_0+g. When $r(i,t)(1-f) \geq 1$, the deme is a source population (rate of change due to per-capita reproduction counteracts the rate of change due to emigration); when $r(i,t)\,(1-f) < 1$, the deme is a sink population (it can not sustain itself without immigration from other streams).

To include the effects of temporally varying environments, we added

$$q\sin\left(\frac{2\pi t}{w}\right)$$

to the per-capita reproduction. This causes per-capita reproduction to change sinusoidally with a maximum change of $2q$ with a w-year period. Such oscillations could be due to events such as El Niño (Pearcy, 1992) and essentially represent changes in the baseline conditions (z_0) over time.

Simulations

We set the baseline per-capita rate of reproduction with z_0=1, g=0.2, and b=0.15. Thus per-capita reproduction was constrained to $0.85 \leq r(i,t) \leq 1.2$. We drew the $z_1(i,0)$ and $z_2(i,0)$ from a gamma distribution with parameters 1 and 1 (Hilborn and Mangel, 1997).

We set f = 0.05 for all populations. This value lies within the ranges found by most of the previously mentioned research on salmonid straying rates. Streams were labeled as sources and sinks on the basis of their initial per-capita rate of reproduction given this straying rate. Therefore, a source population was one with an initial per-capita rate of reproduction greater than or equal to 1.05, and a sink population was one whose rate was less than 1.05. With these parameters, about 40% of the streams were sources and 60% were sinks, as would be the case for a heavily impacted region (Fig. 1). We set m = 0.1.

The initial deme abundance for each stream was assumed to be proportional to the initial per-capita reproduction rate for that stream, even though such relationships may not hold over time (van Horne, 1983). As such, the initial deme abundance, $N(i,0)$, was set equal to $100r(i,0)$. We simulated each metapopulation over a 100-year period, using four scenarios with at least 150 replications for each scenario:

1 All parameters were constant over the 100-year period;
2 Starting in year 5, for all initial source populations ($r(i,0) \geq 1.05$), the good habitat component (z_1) decreased by 5% of its value from the year before, and the bad habitat component (z_2) increased by 5% of its value from the year before.
3 Same as scenario 2, except that all habitats with $r(i,0)>1$ were degraded.
4 Temporally varying environment was incorporated into scenario 2. In this case, the baseline per-capita rate of reproduction (z_0) oscillated between 0.95 and 1.05 over a 20-year period.

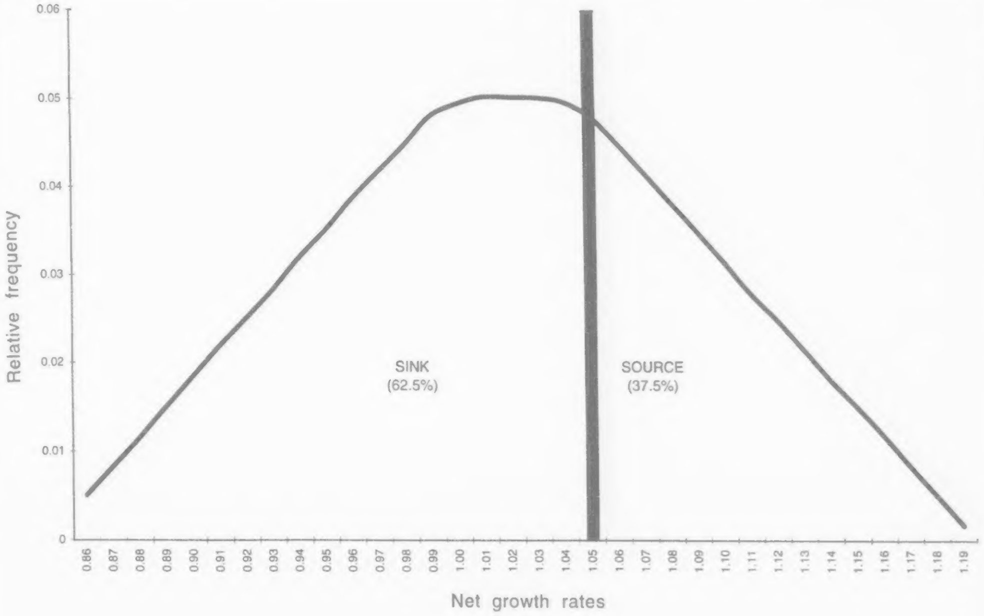


Figure 1

Distribution of net growth rates. Our model generates variation in per-capita growth rates in local populations. A population is a source if its per-capita growth rate exceeds 1.05 and is a sink otherwise.

Results

When habitats are constant over the simulation period, exponential growth occurs 98% of the time. Because no density dependence was incorporated in the model, demes in the source habitats increased exponentially, as did the number of strays from these sources. Such a situation could occur if, for instance, harvesting pressure was decreased on a deme that had been severely overharvested in the past (leading to low abundance) but whose habitat was relatively pristine (maintaining high productivity). This results in all dynamics in the sink populations being obscured by the massive number of immigrants.

It is possible that all the streams constitute sinks (all $r(i,0) < 1.05$); this occurred in 1.3% of the simulations. In this case, there is still the possibility that the metapopulation as a whole could persist for decades before all populations began to decrease (Fig. 2). The reason for this persistence is that individuals that stray are lost only to their natal stream, not to the metapopulation as a whole. The case shown in Figure 2 results when the losses due to some habitats (where $r(i,t)<1$) are nearly offset by production in other habitats (where $r(i,t)>1$). Forty percent of the all-sink metapopulations produced populations that did not decrease over the course of the 100-year simulation. If we had incorporated a parameter to represent decreased reproductive success of strays, the incidence of nondecreasing, all-sink metapopulations would have been lower.

In scenario 2 (Fig. 3), the source populations (demes 3, 4, and 5) initially increased exponentially but eventually began to decrease as the habitat degradation increased. Habitat degradation leads to peaks in local deme abundance (Fig. 4A). The mode of this distribution was around year 20 despite the fact that habitat degradation began in year 5. Furthermore, in over 3% of the sources, deme sizes increased throughout the 100-year simulation.

The population trajectories for the sink habitats were less intuitive (Fig. 3). None of their habitat components changed, yet some demes increased (deme 1) or stayed constant (deme 9) over a number of decades, whereas others decreased. The result depends on the proximity to sources (noting that deme number translates to the location of the deme along the waterway), the per-capita rate of reproduction in those sources, and the sink's own per-capita rate of reproduction. Over 9% of the sink habitats never attained

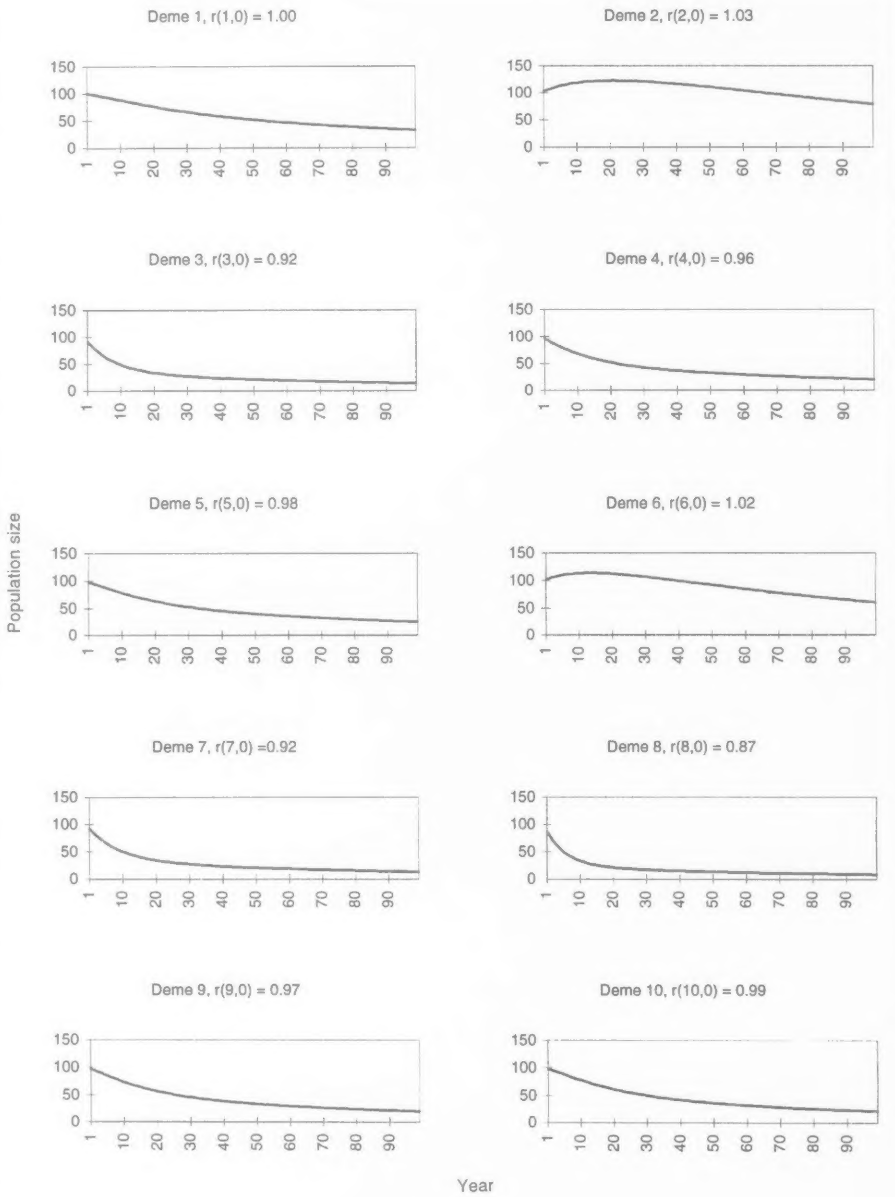


Figure 2

The dynamics of the metapopulation when all local populations are sinks. With scenario 1 or 2 (see "Simulations" section), metapopulation structure and dispersal actually lead to an increase in some population sizes over the short term, before they decline.

deme sizes larger than their initial deme size, but nearly 7% of the demes in sink habitats continued to increase over the entire simulation (Fig. 4B). The fact that deme sizes in some sink habitats do not decrease over the simulation period is a result of the time of the simulation in relation to the rate of habitat degradation in the sources. If the simulations had been longer, all habitats would eventually have reached

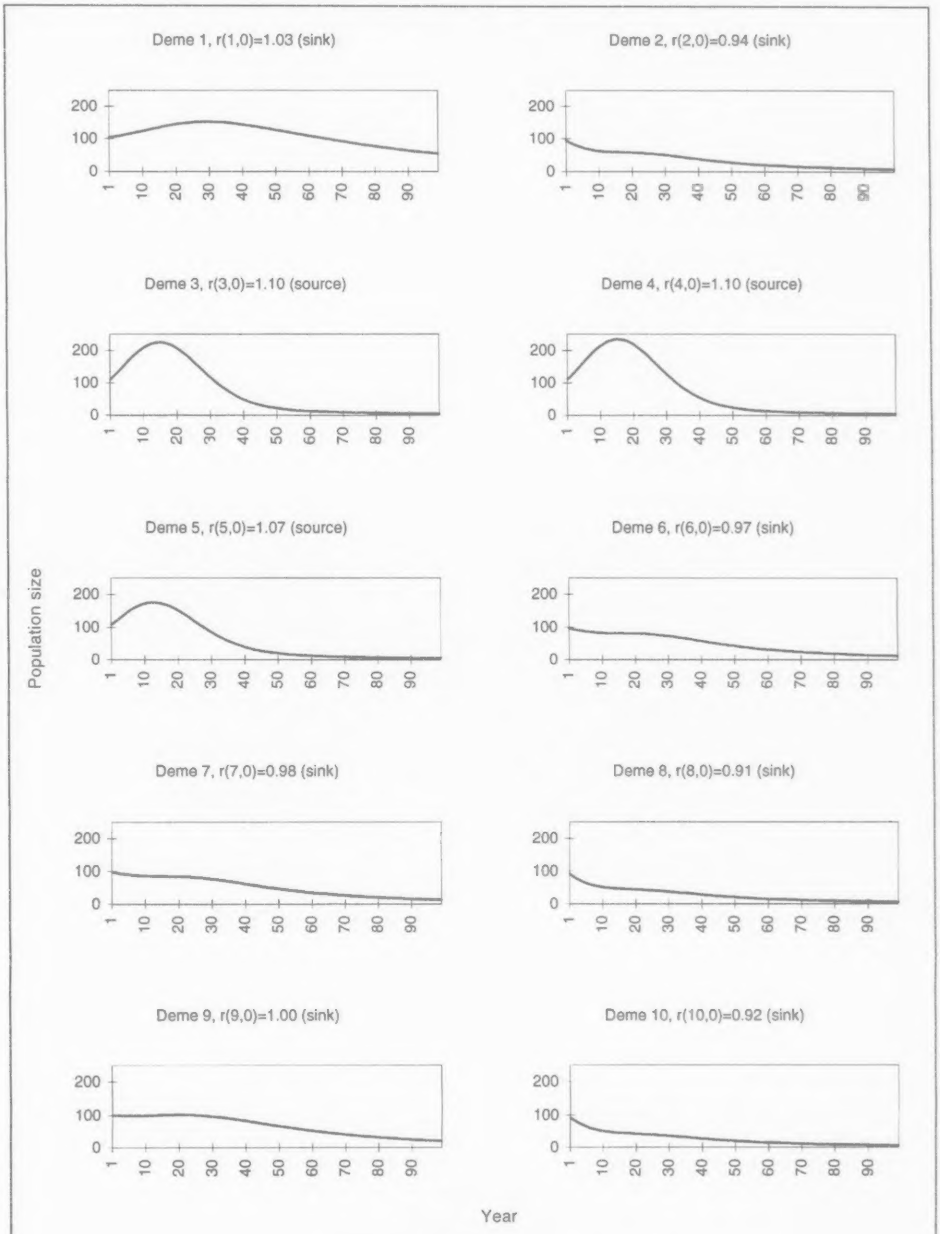


Figure 3

The dynamics of the local populations when some are sources and some are sinks. With scenario 2 (see "Simulations" section), as habitat degradation proceeds (starting in year 5), habitats for source populations slowly become degraded and end up as sinks.

the state of being sink habitats, which would then have resulted in only a few instances of sustained or increasing metapopulations (as described above). Because the number of migrants from one deme to another decreases with distance, the year in which the maximum deme size is attained by the sink decreases as the distance from a source increases; thus the sinks rely on source populations for their viabil-

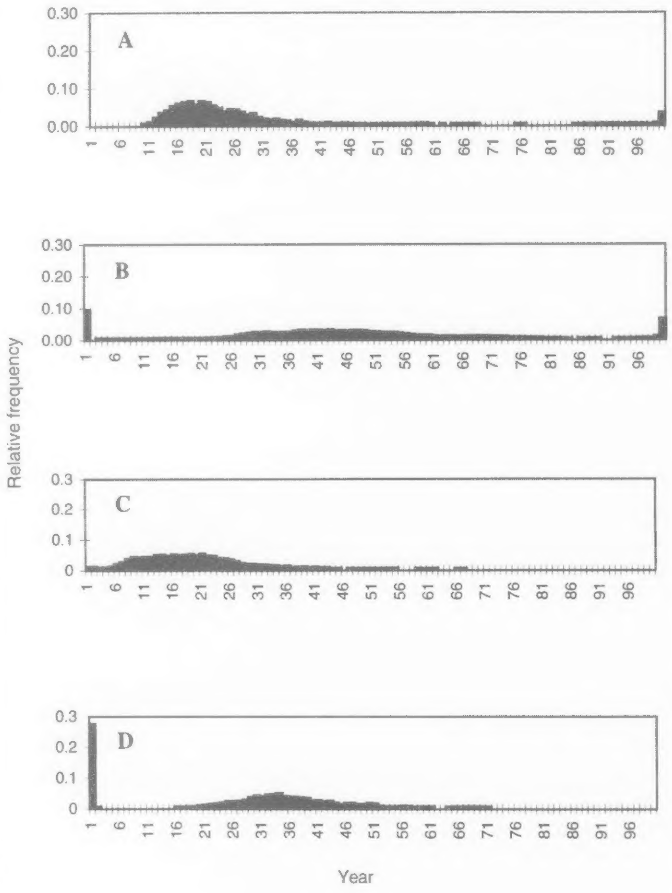


Figure 4

Proportion of sources (**A** and **C**) and sinks (**B** and **D**) attaining their maximum population size in a given year for scenario 2 (A and B) and scenario 3 (C and D). (A) Habitat degradation causes source population size to peak sometime after year 5, although a few populations maintain themselves throughout the 100-year simulation period. (B) About 10% of the sink populations attain maximum size at the start of the simulation. A few attain maximum size at the end of the simulations, but most attain maximum size around year 40. They are supported by source populations. (C) The frequency distribution of peaks in population size for populations with initial per-capita growth rate >1. Compare with Figure 4A. (D) Most populations with initial per-capita growth rate <1 attain peak size at the start of the simulated period. Compare with Figure 4B.

ity (Fig. 5). The variance about these points is due not only to the per-capita reproductive rate of the sink and its nearest source but also to a failure to account for the location of any other sources that may be of equal or greater distance from the nearest source and thus contribute to the sink's dynamics.

When all demes with initial per-capita growth rates greater than one are affected by habitat degradation, declines in deme size occur more frequently, more rapidly, and sooner than in the previous case (Figs. 4 and 6) In this scenario, 100% of the demes were driven towards extinction.

When an oscillating environment is incorporated, the general trends in abundance are similar to those in scenario 2, but now each deme also tracks the environment (Fig. 7). All sources (demes 3, 5, and 7)

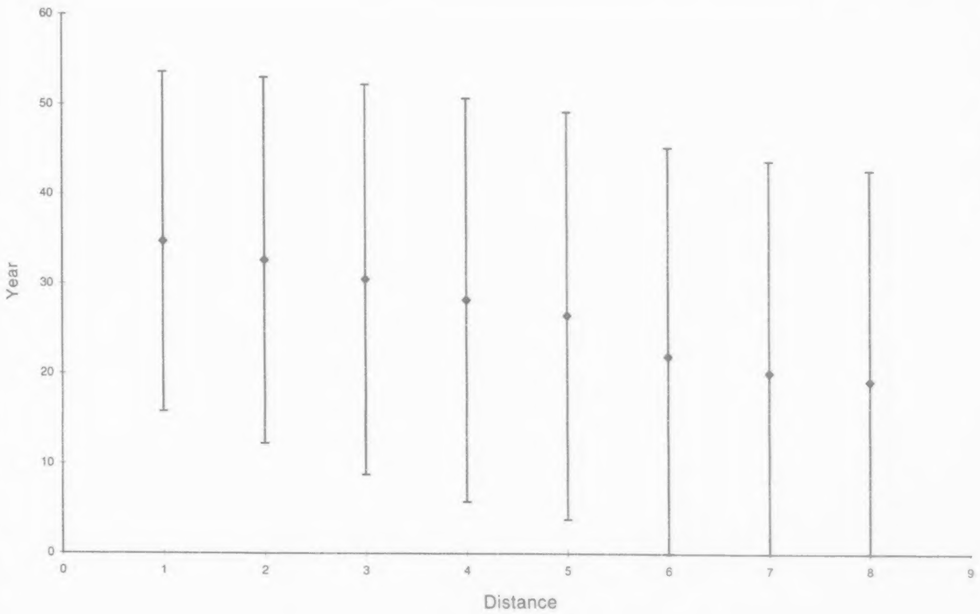


Figure 5

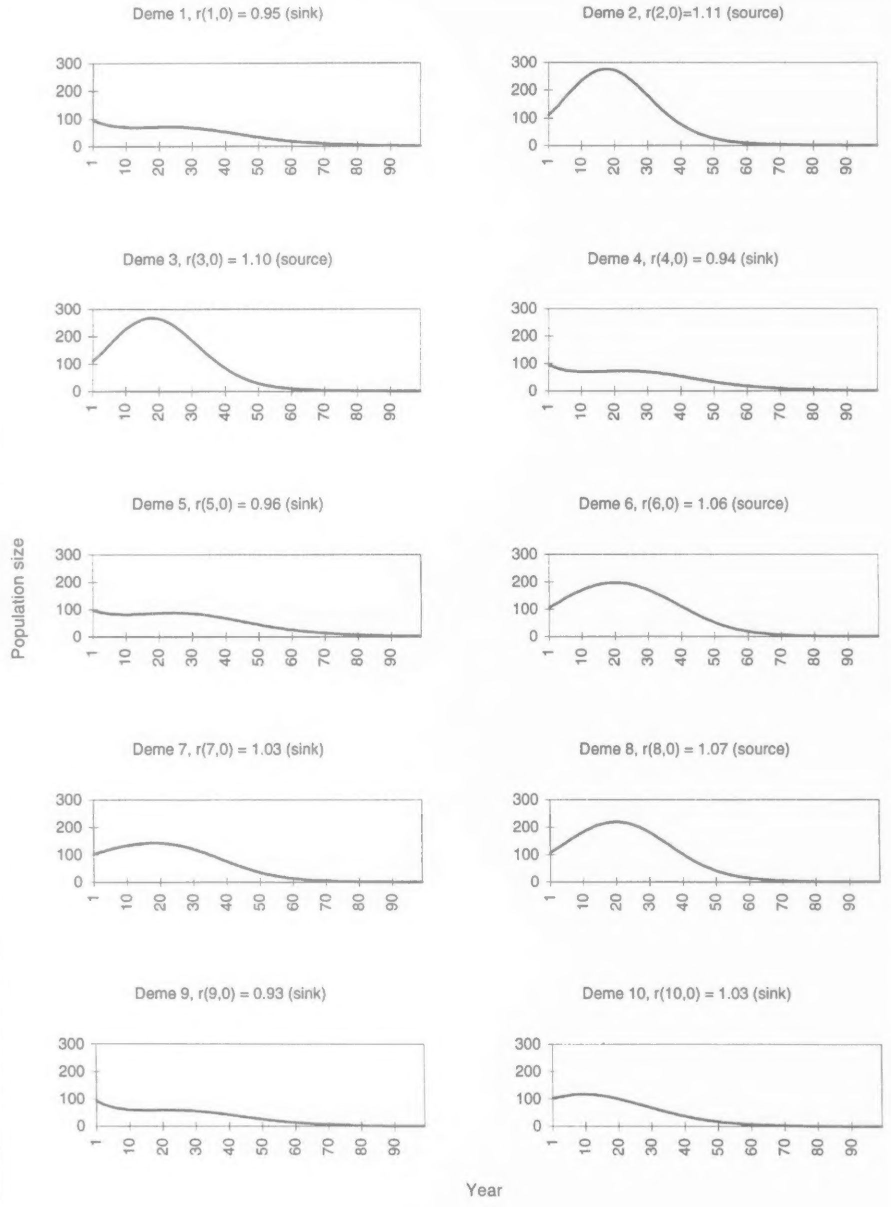
Average year in which sinks attained their maximum population size as a function of the distance to the nearest source. The year in which a sink population attains its maximum size depends upon the distance to the closest source, but there is considerable variation in dependence. Error bars represent one standard deviation.

initially increase but then decrease as habitat degradation progresses. Some demes in sink habitats, such as demes 1 and 4, were relatively stable if not increasing over a fair portion of the simulation period before declining towards extinction.

Discussion

Undetected metapopulation structure in salmonid populations may obscure the signals that managers use to determine the need for convervation action. Abundance trends, either absolute numbers or simple indices of abundance, constitute the primary input into analyses used for fisheries management and decision-making (Hilborn and Walters, 1992). The majority of these techniques assume that the population in question is a closed system, that any immigration or emigration can be considered negligible.

In California, Oregon, and Washington, estimates of population or run size for most salmonid species are commonly based on number of spawning fish or redd counts taken from index reaches or streams (WDFW, 1994; ODFW, 1995; Weitkamp et al., 1995). The absolute numbers of spawning fish or redds counted in these index streams, which incorporate only a minute portion of the available spawning habitat within the watershed, are then used to extrapolate watershed- or basin-level abundance estimates, the very estimates upon which managers base their decisions. In fact, in their discussion on the data available for assessing the population size and risk of extinction for coho salmon along the west coast of the United States, Weitkamp et al. (1995, p. 106) stated ". . . where [stream] surveys were conducted, they are the best local indication we have of population abundance trends." Index reaches and streams such as these are precisely the situation modeled in the specific examples discussed in this paper; straying between these reaches is likely and differential reproductive success between strays and natal fish may not occur. The NMFS's analysis of coho salmon populations considered short- and long-term trends in abundance to be the main indicators for the risk of extinction but avoided using estimates based on index streams (Weitkamp et al., 1995). Using the trends in abundance for an entire ESU, Weitkamp et al. (1995) attempted to avoid the problems associated with the


Deme 1, r(1,0) = 0.95 (sink)

Deme 2, r(2,0)=1.11 (source)

Deme 3, r(3,0) = 1.10 (source)

Deme 4, r(4,0) = 0.94 (sink)

Deme 5, r(5,0) = 0.96 (sink)

Deme 6, r(6,0) = 1.06 (source)

Deme 7, r(7,0) = 1.03 (sink)

Deme 8, r(8,0) = 1.07 (source)

Deme 9, r(9,0) = 0.93 (sink)

Deme 10, r(10,0) = 1.03 (sink)

Figure 6

The local population dynamics when all populations with initial per-capita growth rate >1 are subject to habitat degradation (scenario 3 in "Simulations" section). Compare with Figure 3.

assumption of a closed-system. However, depending on the time scale of the data available and the decrease in reproductive success for strays, undetected metapopulation structure could still cause problems. The second problem arises because metapopulation structure can disconnect the abundance-habitat quality relationship. This could lead managers to make erroneous inferences regarding the habitat requirements for a species. The

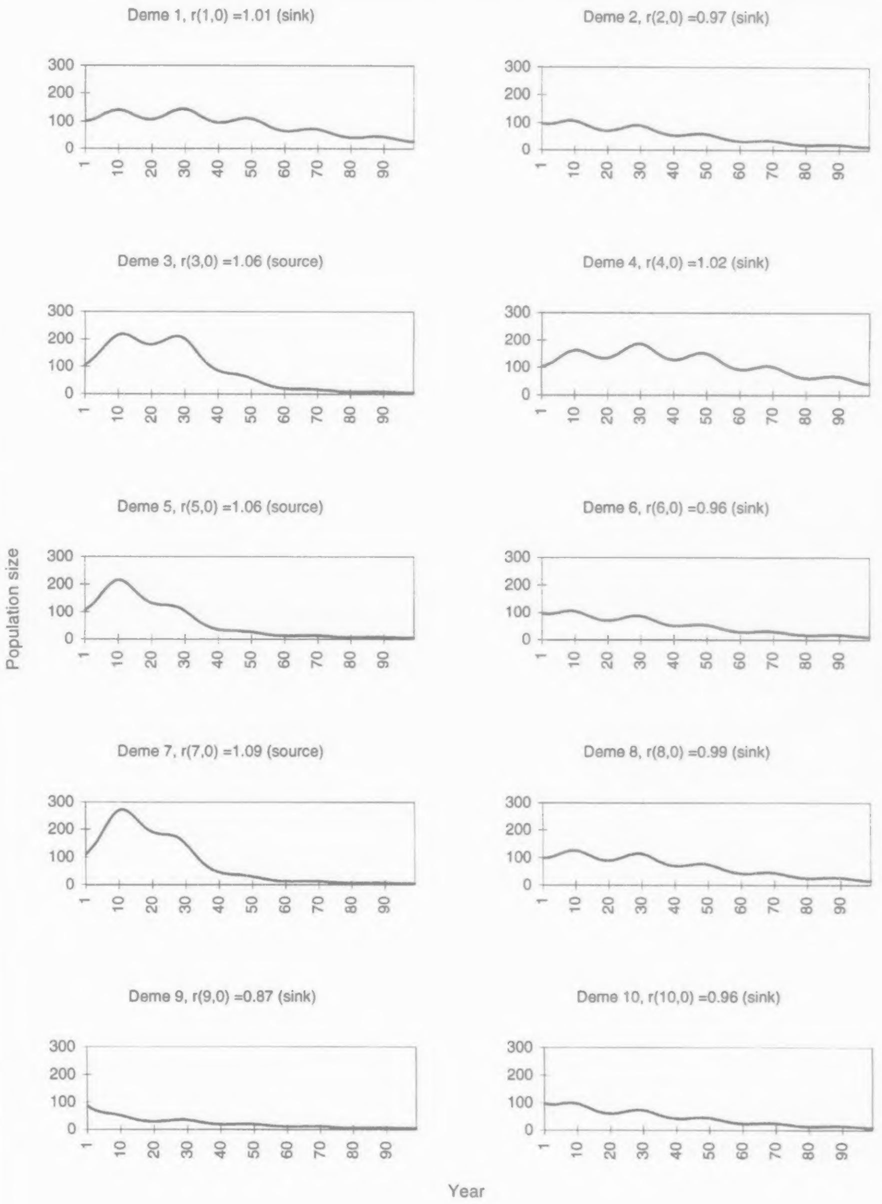


Figure 7

When z_0 varies (scenario 4 in "Simulations" section), the local population sizes reflect such variation. Compare with Figure 3.

sample metapopulations from the simulations provide demonstrations of how this may occur.

Figure 3 demonstrates one example where metapopulation structure could obscure management signals. Keep in mind, there is neither density dependence, observation error, nor stochasticity in the population dynamics, and a deme could represent an index reach (conforming to our uniform reproductive success assumption) or an entire stream (where the uniform success assumption may be less accurate). If a manager had the entire time series data for all of the demes, the problem (though not the solution) would be evident; all demes would have declined significantly. Suppose, however, the manager is currently in year 30, and has only 25 years of data (years 5–30). Over that time period, all demes in sink habitats would be relatively stable or decline only slowly, even though none could sustain themselves without immigrants. In fact, deme 1 had been increasing until year 30. The demes in the source habitats, however, showed the effects of habitat degradation. Seeing these trends, the manager could perhaps stabilize these demes and thus inadvertently save the entire metapopulation. Still, the true risk for the sink populations would be unknown to the manager. The sink populations would appear stable not because they were in good condition but rather because of their interconnectedness with one another and the source populations.

Rieman and McIntyre (1995) suggested that a similar process is occurring with bull trout (*Salvelinus confluentus*) populations in Idaho. Although bull trout were found to use small streams, they do so only at a very low frequency. Rieman and McIntyre (1995) concluded that the presence of trout in these streams may be influenced by habitat preference but that these populations depend on dispersal of individuals from larger streams for their sustainability.

The addition of a varying environment clouds the picture even more (Fig. 7). The manager must now distinguish between decreases due to environmental factors and decreases due to factors that can be controlled. Imagine a manager starting in year 1. How can one recognize that the metapopulation is collapsing due to anthropogenic effects and not simply to environmentally induced effects? When would the alarms sound? Probably not until sometime after year 30, when even the most historically productive demes do not begin to increase. Seven out of ten of the demes could not maintain themselves without immigration, there is neither observation error nor stochasticity, and it would still take over 25 years of habitat degradation before the problem was noticed and the alarms sounded.

These problems become even more serious when management boundaries do not coincide with metapopulation boundaries or when only a portion of the metapopulation is used as index streams, as is likely the case. In such a situation, a manager will be concerned with, have jurisdiction over, and maybe have data on some subset of the metapopulation. Returning to Figure 3 (where managers do not have to deal with fluctuating environments), imagine if a manager had responsibility, and therefore data, for only demes 6, 7, 8, 9, and 10, which are nevertheless a significant portion of the metapopulation. Between years 5 and 30, all demes were relatively stable, despite the fact that without immigration, even the most productive deme (deme 9) would decrease at a rate of 5% per year. After year 30, all these demes begin to decline. The manager would, of course, begin looking at these demes to try and see what was causing this decline; a good manager would try to find what had changed. In fact, nothing has changed with these demes; they have exactly the same rates of per-capita reproduction and straying over the entire simulation. Only the number of immigrants has changed. Without looking beyond their own jurisdiction or at streams other than the index streams, managers would not find the true cause for the change in dynamics. As the number of demes that are used as index streams or that lie within a manager's jurisdiction decreases, the likelihood of such a problem increases. Considering that over 90% of the sink populations increased in size during some portion of the simulation time horizon (i.e. their maximum size was reached sometime after year 1, Fig. 4B), the fate of sink populations has as much, if not more, to do with the health of the demes in other habitats as with the quality of their own habitat.

Another problem associated with undetected metapopulation structure arises directly from this last example. A manager may see a change in the dynamics in the populations and look for the cause. However, the cause of this change is outside the manager's jurisdiction or data set; it is not local. If the manager looks only for local causes for this change, she or he is likely to find some variable that is correlated with this cause and possibly infer local causality. Having attributed causality to a local variable, the manager would likely start funding projects to fix the perceived problem in the correlated variable. If one is lucky, very lucky, this variable might have some relationship to the per-capita reproductive rate and thus improve the situation a bit. This might, then, slow the rate of decline, but because it is not the true cause of the decline, the situation would likely continue to deteriorate. How much of a manager's limited resources might be spent on such activities before the true causal relationship was discovered? The study by Gowan and Fausch (1996) suggests that this problem may be occurring with habitat enhancement projects for trout in Colorado; managers promote the addition of woody debris in streams because it increases trout density, even though it does not seem to improve the demographic parameters of the population.

Including density dependence (as in Ricker stock-recruitment relationships) and observation or process uncertainty (Hilborn and Mangel, 1997) in the model will not change any of the main conclusions. These factors will make recognizing the problem even more difficult, as is the case in the real world. To uncover metapopulation dynamics, one must explore two aspects of each population's life history in reference to its habitat: dispersal (in the form of immigration and emigration) and the per-capita reproductive rate (defined by survival and reproduction). Watershed-scale estimates of these rates, however, are not appropriate. Given their reliance on index stream counts, managers must know the rates of immigration, emigration, and reproduction specific to that stream to be able to understand the true dynamics of that stream. The dispersal of individuals is important to determine the extent of the metapopulation structure. The focus should be both on absolute numbers as well as on the effective migration rates that account for differences in survival and productivity between the residents and the migrants. Survival and reproduction estimates (the components of the per-capita reproductive rate) will allow the manager to assess the potential importance of the metapopulation structure (i.e. to define sources and sinks). As long as the risk exists for abundance and density estimates to be disconnected from habitat quality and per-capita reproduction, all the above information is required to make an accurate assessment of the conservation status of the individual demes and to choose the appropriate management actions.

A great deal of time, money, and effort is currently directed toward the conservation and improvement of salmonid populations and their habitats. The NMFS report alludes to the fact that metapopulation structure may exist between some salmonid populations, and the NRC (1996) report lists the maintenance of metapopulation structure as one of its most important recommendations. Without investigating the possibility of metapopulation structure, researchers, managers, and policy makers are setting themselves up to fall into the traps described above: that of either not seeing a problem that may exist or, if they do see it, not knowing the true causes of such a problem.

Acknowledgments

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Age and growth estimates for New Zealand hapuku, *Polyprion oxygeneios*

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Abstract.–*Polyprion oxygeneios* (family Polyprionidae) is fished commercially and recreationally in the southern Indian and Pacific Oceans. Estimates of growth rate, age at maturity and recruitment, and longevity are required for fishery management. We used thin otolith sections to age *P. oxygeneios* from New Zealand, where it is known as hapuku. Growth bands were difficult to count, leading to low counting precision and, for some age groups, to a small between- and within-reader ageing bias. These problems, however, had little effect on the shape of growth curves fitted to length-at-age data. An oxytetracycline injection experiment supported our hypothesis of annual deposition of an opaque-hyaline band pair, but further validation is required. Independently derived von Bertalanffy growth curves (from length-frequency data) and growth-rate estimates (from tag-recapture data) for young hapuku agreed well with estimates from length-at-age data.

Juvenile hapuku are pelagic and most switch to a demersal habitat at around 50 cm total length and at an estimated age of 3–4 years. They probably recruit to commercial trawl catches at about the same age. Female hapuku appear to grow slightly faster than males. Both sexes mature at about 10–13 years. The longevity of hapuku is uncertain, but some individuals probably live longer than 60 years.

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Fish. Bull. 97:227–242 (1999).

Polyprion oxygeneios (Schneider, 1801) (family Polyprionidae) is a large demersal fish that inhabits temperate and subtropical waters of the southern Indian and Pacific Oceans (Roberts, 1986; Fig. 1). It supports significant fisheries off the Juan Fernández Islands, Chile, and off New Zealand and is an important bycatch in south-east Australian longline fisheries (Johnston, 1983; Pavez and Oyarzún, 1985; Pizzaro and Yáñez, 1985; Kailola et al., 1993; Annala and Sullivan, 1997). The closely related wreckfish, *P. americanus* (Bloch and Schneider, 1801) is found in the North and South Atlantic Oceans, Mediterranean Sea, southern Indian Ocean, and south-west Pacific Ocean (Roberts, 1986; Sedberry et al., 1994) and supports fisheries throughout its range (Sedberry et al., 1994, 1996).

The ability to age *Polyprion* species is essential for proper management of their widespread fisheries, because it will enable determination of growth rates, ages at maturity and recruitment, longevity, and natural mortality rates. Previous attempts to age the two species have had limited success. Age and growth of *P. oxygeneios* have been estimated from otolith band counts in New Zealand (McDougall, 1975) and from scale annuli counts in Juan Fernández Island (Pavez and Oyarzún, 1985). A study on the age and growth of *P. americanus* from the north-west Atlantic is currently underway (Sedberry et al., 1994, 1996; Manooch and Potts[1]). However, otolith bands have proven difficult to count in both species, scale annuli are unreliable for older fish, and the ageing techniques have not been validated.

In New Zealand, *P. oxygeneios* and *P. americanus* are managed as a single species-unit in the Quota Management System (QMS) (Paul and Davies, 1988; Annala and Sullivan, 1997). Both species are fished commercially and recreationally throughout New Zealand. They are highly sought after, but catches are relatively low. Commercial landings of both species combined peaked at 2700 t in 1983–84, but since the introduction of the QMS, they have been constrained by quotas to less than 1500 t per year (Annala and Sullivan, 1997). Despite these quotas, commercial line and set-net fisheries for *Polyprion* species have been seasonally important for small inshore fishing vessels in many parts of New Zealand. Annual recreational landings were about 500 t in 1991–94 (Annala and Sullivan, 1997).

This paper addresses age and growth in New Zealand *P. oxy-*

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[1] Manooch, C. S., and J. Potts. 1997. National Marine Fisheries Service, 101 Pivers Island Rd, Beaufort, NC 28516. Personal commun.

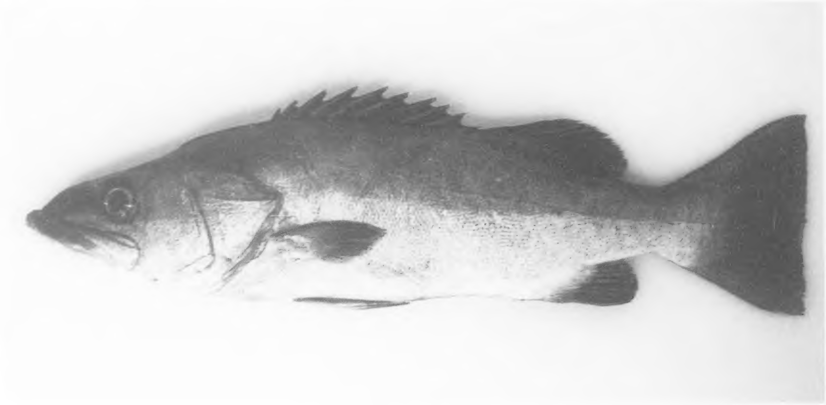

Figure 1
Hapuku, *Polyprion oxygeneios* (63 cm TL).

geneios, hereafter called hapuku. However, our results are also relevant to other populations of *P. oxygeneios* and, because both species of *Polyprion* have similar otolith structure, our results should also assist in the interpretation of otoliths of *P. americanus*. We used thin otolith sections to age hapuku and attempted to validate ages using oxytetracycline (as a time marker) and otolith marginal state analysis. We also obtained independent growth rate estimates from length-frequency and tag-recapture data for comparison with growth rate estimates derived from length-at-age data.

Materials and methods

Otolith ageing

Sagittal otoliths were obtained from 1400 hapuku collected from waters off New Zealand, from 1979 to 1995. Many otoliths were collected during studies by Johnston (1983) and Roberts (1986) and made available to us. Since then, additional otoliths have been collected by us during research trawl surveys and sampling trips aboard commercial line vessels, as well as by Ministry of Fisheries scientific observers aboard commercial line and trawl vessels.

Most otoliths were accompanied by information on fish total length (TL, to the centimeter below actual length) and sex. Three subsamples of these otoliths were selected for analysis. The first comprised 44 otoliths collected from five sites between Three Kings Islands and Great Barrier Island (Fig. 2) (hereafter called the "northern" sample). The second consisted of 178 otoliths collected from Cook Strait and Kaikoura (Fig. 2; "central" sample) and the third consisted of 28 otoliths from large hapuku collected from other sites throughout New Zealand ("miscellaneous" sample), selected to boost the number of old fish in the data set.

One otolith from each pair was viewed under transmitted polarized light, and the straightest dorsonuclear ridge was marked with a pen to guide the saw for sectioning. Each otolith was then embedded in a block of clear epoxy resin and sectioned transversely through the core at a thickness of 650 µm by using a dual-blade high-speed diamond saw. One face of the section was polished with carborundum paper and glued on to a microscope slide with thermoplastic cement. The opposite face was then ground and polished to a final thickness of 200–350 µm, depending on the clarity of the otolith bands when viewed under both reflected and transmitted light.

Opaque otolith bands were counted under transmitted light in the dorsal part of each section by two readers. Both readers carried out an initial training exercise by making counts on a subsample of the sections, while knowing the collection details of each fish (TL, sex, and site), and then discussed their results. Subsequent counts were carried out "blind"; i.e. the readers did not know the size, sex, or collection site of the hapuku. Reader 1 counted all sections once (R_1) and reader 2 counted all sections twice, the two counts being separated by two months ($R_{2,1}$ and $R_{2,2}$). The readability of sections was scored on a scale from 1 (unreadable) to 5 (exceptionally clear).

Otolith band counts were assessed for ageing bias and precision (between readers, and between read-

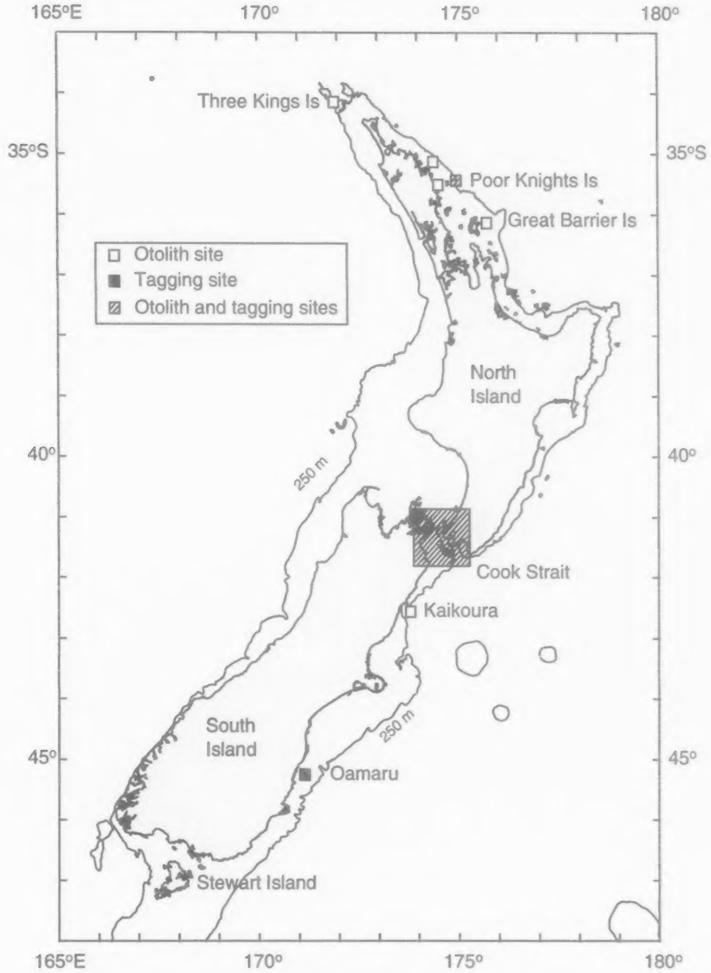
165°E
170°
175°
180°
35°S
40°
45°
Three Kings Is
Poor Knights Is
Great Barrier Is
☐ Otolith site
■ Tagging site
▨ Otolith and tagging sites
North Island
250 m
Cook Strait
Kaikoura
South Island
250 m
Oamaru
Stewart Island

Figure 2

Hapuku otolith collection sites and tag-release sites.

ings by reader 2) by using age-bias plots and plots of the coefficient of variation (CV) against age, as recommended by Campana et al. (1995). These two plots show the means (and their standard errors), and the CVs, respectively, of the band counts made by reader x for each "age" as determined by reader y. For example, for all the hapuku that were judged by reader y to have 10 bands, the mean, standard error, and CV were calculated from the band counts made by reader x for the same fish, and plotted at age 10 on the x-axis. Age estimates made by reader 2 on the second reading ($R_{2,2}$) were selected as a baseline against which to compare other estimates because it was anticipated that the experience gained during the first reading would produce more reliable age estimates during the second reading.

Validation of the annual formation of otolith bands was attempted by marginal increment analysis and oxytetracycline injection. The marginal composition of 76 otoliths from northern and central hapuku, aged 3–8 years, was graded as opaque, narrow hyaline, or wide hyaline. The classification of hyaline zones as narrow or wide was based on a comparison of the marginal zone width with the width of the preceding hyaline zone. A qualitative classification was used because the presence of split opaque bands made it difficult to measure the marginal increment. The data were grouped into two-month intervals because not all months were sampled and because sample sizes were small.

Thirty-nine hapuku were tagged (see "Tag-recapture" section), injected intramuscularly with oxytetracycline hydrochloride (OTC), and released at the Poor Knights Islands (Fig. 2). Two OTC brands and dosage rates were used: 27 fish were injected with terramycin at a dosage rate of 80 mg/kg; and 12 were injected with engemycin at 35 mg/kg. Five OTC-injected fish were recaptured and their otoliths removed. One otolith from each pair was sectioned as described above and viewed under transmitted white light and reflected UV light. The composition of the otolith (number of opaque or hyaline bands) outside the OTC mark was determined, and the amount of new otolith material laid down along the dorsonuclear axis was measured.

Growth curves were fitted to the length-at-age data bu using the von Bertalanffy growth model:

$$L_t = L_\infty\left(1-e^{-K[t-t_0]}\right),$$

where L_t = the expected length at age t years;
L_∞ = the asymptotic maximum length;
K = the von Bertalanffy growth constant; and
t_0 = the theoretical age at zero length.

Length-frequency distributions

Hapuku length-frequency distributions were obtained from a series of four bottom trawl surveys conducted from the research vessel *Tangaroa* (towing a 60-mm mesh codend) off Southland (the southern coast of South Island and the Stewart Island shelf between latitudes 46–49°S). The surveys were carried out annually in February and March, 1993–96, and covered a depth range of 30–600 m. Further details of the surveys are provided in the studies of Hurst and Bagley (1994) and Bagley and Hurst (1995, 1996a, 1996b).

Von Bertalanffy growth curves were fitted to the four length-frequency distributions by using the MULTIFAN model (Fournier et al., 1990). This model analyses multiple length-frequency distributions simultaneously and uses a maximum likelihood method to estimate the number of age classes represented by the data, the proportions of fish in each age class, and the von Bertalanffy growth parameters L_∞ and K. The main assumptions of the MULTIFAN model are the following: 1) the lengths of the fish in each age class are normally distributed around their mean length; 2) the mean lengths-at-age lie on or near a von Bertalanffy growth curve; and 3) the standard deviations of the actual lengths about the mean length-at-age are a simple function of the mean length-at-age (Fournier et al., 1990).

The growth parameters were estimated by conducting a systematic search across a parameter space of plausible K values (0.005–0.30) and age classes (6–15). It is possible to constrain the MULTIFAN search further by specifying initial estimates for the mean length-at-age, and the range of the mean length, for one or more age classes (Fournier et al., 1990). However, this is not necessary when the length distributions contain adequate modal structure; therefore such constraints were not used in this study.

For each of the identified age classes, MULTIFAN also estimates the ratio of the last to first length standard deviations (S_R) and the geometric mean of the first and last standard deviations (S_A). The MULTIFAN model was fitted for two different growth hypotheses: 1) constant length standard deviation for all age classes (fitted by setting S_R=1 and estimating S_A); and 2) variable length standard deviation across age classes (fitted by estimating both S_A and S_R). Because all four trawl surveys were conducted at the same time of year, the data contain no information on seasonal variability of growth, and no seasonal parameters were fitted.

Each combination of K and the number of age classes constituted a model fit. The constant standard deviation hypothesis was fitted to the data first, followed by the addition of the parameter for variable standard deviation. For each combination of K, number of age classes, and growth hypothesis, the maximum log-likelihood (λ) was calculated. Likelihood ratio tests were used to test for significant improvement in model fit. Twice the increase in λ is distributed as a χ^2 distribution with degrees of freedom equal to the number of additional parameters. Following Fournier et al. (1990), a significance level of 0.10 was used for testing whether there was any gain in introducing an additional age class in the length-frequency analyses. The test for improvement resulting from the addition of the parameter for variable standard deviation was carried out with a significance level of 0.05.

The von Bertalanffy growth parameter t_0 was estimated from the equation

$$t_0 = t_1 - a_1,$$

where a_1 = the age estimated by MULTIFAN (in years since zero length) of the youngest age class at the time it first appeared in the length-frequency samples; and
t_1 = the time elapsed in years between the theoretical birthday and the first appearance of the youngest year class in the samples.

The theoretical birthday was defined as 1 September based on observations of prespawning fish in June–August and postspawning fish in October–December (Johnston, 1983; Roberts, 1986).

Tag recapture

1623 hapuku were tagged at three main sites: Poor Knights Islands (July 1987–August 1989, n=106), Cook Strait (August 1979–June 1984, n=599) and Oamaru (March 1988–April 1990, n=918) (Fig. 2). Fish were caught by longline or drop (dahn) line in depths less than 160 m. Only lively fish without everted stomachs or bulging eyes were tagged. Distended swimbladders were vented by means of a hollow needle inserted through the wall of the body cavity. Hapuku were measured (TL), tagged with a loop, dart, or spaghetti tag, and released. Oamaru hapuku were double tagged with both a loop and a dart tag. Loop and spaghetti tags were inserted through the muscle just anterior to the dorsal fin and clipped or tied together, and dart tags were inserted into the muscle directly below the first dorsal-fin ray. Each tag was printed with a serial number, a return address and notice of a reward. Recapture data and most measurements of recaptured hapuku were provided to the Ministry of Agriculture and Fisheries by the fishermen who caught them, but occasionally whole fish were returned for measurement.

Von Bertalanffy growth estimates were obtained from the tagging data by using the maximum likelihood method and the computer program GROTAG (Francis, 1988). GROTAG also estimates g_α and g_β, the mean annual growth of fish of lengths α and β respectively. The reference lengths α and β were chosen to lie within the range of lengths of tagged hapuku. Francis (1988) showed that these parameters describe the growth information in tagging data better than the more conventional von Bertalanffy growth parameters L_∞ and K do. The expected length increment, ΔL, for a fish of initial length L_1 at liberty for time ΔT is given by

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1 \right] \left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T} \right].$$

Also estimated were m and s (the mean and standard deviation of the measurement error), v (the coefficient of variation of growth variability), and p (the proportion of outliers) (Francis, 1988). Preliminary GROTAG fits suggested that the von Bertalanffy growth model was not appropriate for tagged hapuku; therefore a linear GROTAG function with only one growth parameter (g_α) was fitted to the data. A seasonally varying growth function was also tested. Differences in growth rate between the two sexes in Cook Strait (the sex of recaptured fish was not determined for the other two areas) and among the three tagging areas were also investigated.

The approach used was to fit a simple GROTAG model with few parameters to the data. The complexity of the model was then gradually increased by introducing additional parameters (for example, parameters to allow for seasonal variation in growth). At each stage, new parameter estimates were made and likelihood ratio tests for significant improvement in model fit were carried out as described above for MULTIFAN models. A significance level of 0.05 was used for testing whether there was any gain from introducing additional parameters.

Results

Otolith ageing

Otolith structure The otoliths of the hapuku we examined had an opaque core (dark in transmitted light) and an opaque line that radiated along the dorsoventral axis (Fig. 3). The line was usually split by 1–3 hyaline bands (light in transmitted light). The sulcus was also mostly opaque. The remainder of the otolith consisted of alternating opaque and hyaline bands. In young fish, the hyaline bands were wider than the opaque bands, but difference in width declined in older fish. Opaque bands usually consisted of multiple, fine, wavy opaque and hyaline zones (Figs. 3 and 4A). The demarcation between each compound opaque band and the adjacent hyaline bands was often indistinct, making the bands difficult to count. The banding pattern was usually clearest in the dorsal half of transverse otolith sections. We used counts of the compound opaque bands as age estimates.

Five otolith sections were considered unreadable, and a further four otoliths were lost or damaged during preparation. Of the remaining 241 otoliths, 78% were scored as poor or moderate (readability 2 or 3); only 22% were good or exceptionally clear (readability 4 or 5).

Validation Otolith marginal state was difficult to assess because of the presence of split opaque rings. There was no apparent seasonal cycle in marginal composition, and sample sizes in most two-month periods were inadequate to provide good estimates of the percentage of the population with opaque margins (Jan–Feb percent opaque=50.0, n=14; Mar–Apr 37.5, 8; May–Jun 36.4, 33; Jul–Aug 42.9, 7; Sep–Oct 50.0, 10; Nov–Dec 25.0, 4). The same conclusion was reached for the central data alone (n=50).

Five OTC-injected hapuku were recaptured after 0.20–2.66 years at liberty (Table 1). All had distinct, bright OTC bands when viewed under UV light (Fig. 4B). There was no apparent relation between OTC

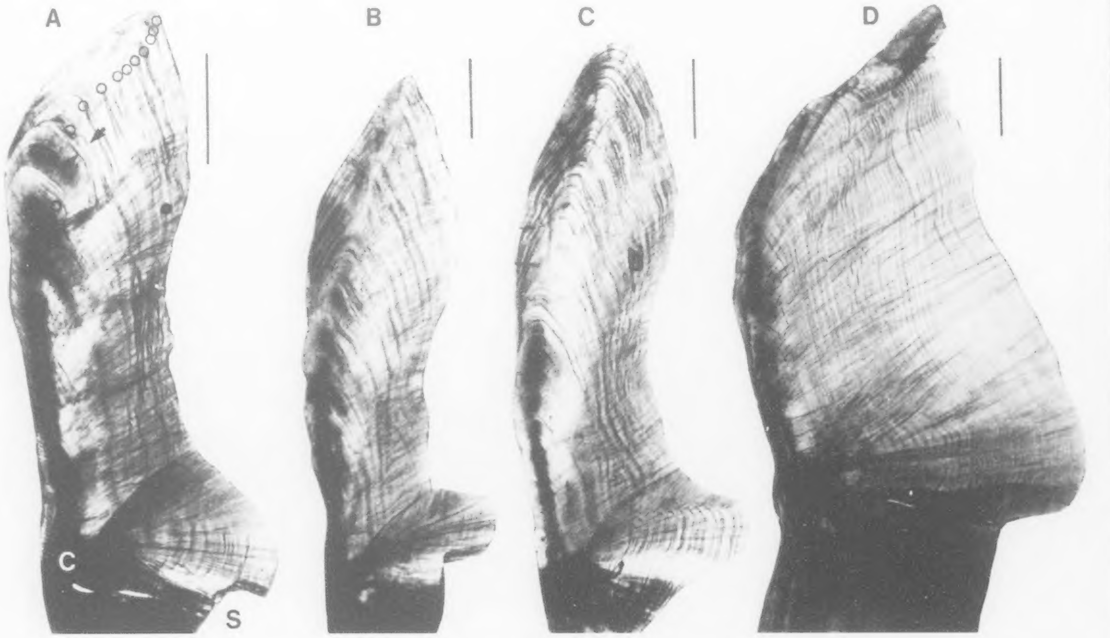

Figure 3

Photomicrographs (transmitted white light) of the dorsal halves of transverse sections of hapuku otoliths from (**A**) an 85-cm female, northern, readability 3, estimated age (mean of R_1, $R_{2.1}$ and $R_{2.2}$) 11.7 years; C = core, S = sulcus, arrows indicate a compound opaque band, circles indicate opaque bands; (**B**) an 87-cm female, Cook Strait, readability 4, age 14.7 years; (**C**) a 106-cm male, Cook Strait, readability 4, age 19.0 years; (**D**) an 121-cm male, Kaikoura, readability 5, age 45.7 years. Scale bars = 1 mm.

Table 1

Details of recaptured hapuku that were tagged and injected with oxytetracycline (OTC). M = male, T = terramycin, E = engemycin, — = not determined. Increment width is the amount of postinjection otolith material deposited along the dorsonuclear otolith axis. Increment pattern is the type of material (O=opaque, H=hyaline) laid down between the OTC mark (m) and the otolith margin. An "I" subscript indicates an incomplete band, and a question mark indicates uncertainty in determining the composition of the otolith margin.

Tag number	Length at tagging (cm)	Length at recapture (cm)	Sex	OTC brand	Date tagged	Date recaptured	Years at liberty	Increment width (mm)	Increment pattern
SGO306	89	104	M	T	20 Oct 87	19 June 90	2.66	0.61	mO_IHOHOH
SGO322	85	87	M	T	8 Jul 88	21 Dec 88	0.45	0.08	mO_IH_I
SGO328	55	55	—	E	27 Oct 88	10 Mar 89	0.37	0.16	mO_IH_I
SGO329	73	77	—	E	2 Dec 88	12 May 89	0.44	0.05	mHO_I?
SGO340	68	65	—	E	2 Jul 89	14 Sep 89	0.20	0.01	mO_IH_I?

brand (terramycin or engemycin) or dosage and the width or intensity of the OTC mark. Four hapuku injected with OTC in July–October showed an OTC mark that fell within an opaque band, indicating that opaque bands are formed in the austral winter–spring. The remaining fish was injected in December and had an OTC mark at the distal edge of an opaque band, indicating that hyaline band formation begins in spring–summer.

The OTC results from all five hapuku are consistent with the deposition of one hyaline-opaque band pair on the otolith each year. The hapuku that had

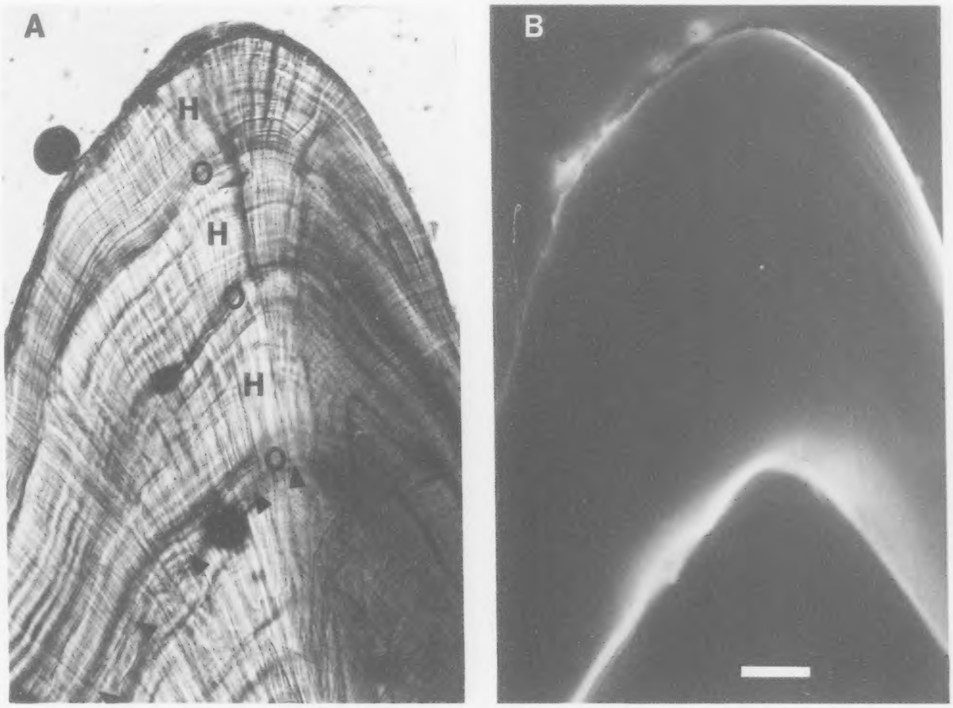

Figure 4

Photomicrographs of the dorsal end of a transverse section from a hapuku otolith illuminated by (**A**) transmitted white light, and (**B**) reflected UV light. The hapuku had been tagged, injected with oxytetracycline, and recaptured after 2.66 years at liberty (see Table 1, tag number SGO306, for further details). Arrowheads indicate the position of the inner edge of the oxytetracycline mark, which lies within an opaque band. Outside that band are three hyaline (H) and two opaque (O) bands. Scale bar = 0.1 mm.

been at liberty for the shortest time (SGO340, 0.20 years) had the OTC mark near the margin (postinjection increment width along the dorsal axis=0.01 mm) (Table 1). Three hapuku with intermediate periods at liberty (0.37–0.45 years) had moderate postinjection otolith increments of 0.05–0.16 mm. SGO328, which was the smallest of the three hapuku at tagging, had the largest increment. SGO322 and SGO328 each had an incomplete opaque band and an incomplete hyaline band outside the OTC mark. SGO329 had a complete hyaline band and possibly an opaque band beginning to form at the margin near the dorsal tip of the otolith. A hapuku that had been at liberty for 2.66 years (SGO306) had a wide postinjection increment (0.61 mm) consisting of a partial opaque band followed by three hyaline and two opaque bands (Fig. 4; Table 1).

Age estimates and growth rates $R_{2,1}$ and $R_{2,2}$ were strongly positively correlated (coefficient of multiple determination [R^2]=94.6), although they differed markedly for some individuals (Fig. 5A). Some of the larger differences were for otoliths that were judged difficult to count (readability 2), but large differences were also found for clearer otoliths (readability 3–5). $R_{2,1}$ tended to be higher than $R_{2,2}$ for fish aged 3–18 years in $R_{2,2}$ (mean difference=1.0 years) (Fig. 6A). Sample sizes were small for hapuku older than 18, but it appears that the same bias occurred for them.

Age estimates made by both readers (R_1 and $R_{2,2}$) were also highly correlated (R^2=92.4) but there were some substantial differences (Fig. 5B). There was no apparent bias between the two sets of estimates for hapuku aged 3–12 in $R_{2,2}$, but there was a slight tendency for $R_{2,2}$ to exceed R_1 over the range 13–18 years (Fig. 6B).

Ageing precision was low and variable, both within and between readers, for hapuku aged 3–18 years (Fig. 7). The CV of the age estimates was slightly lower between the two readings of reader 2 ($R_{2,1}$ ver-

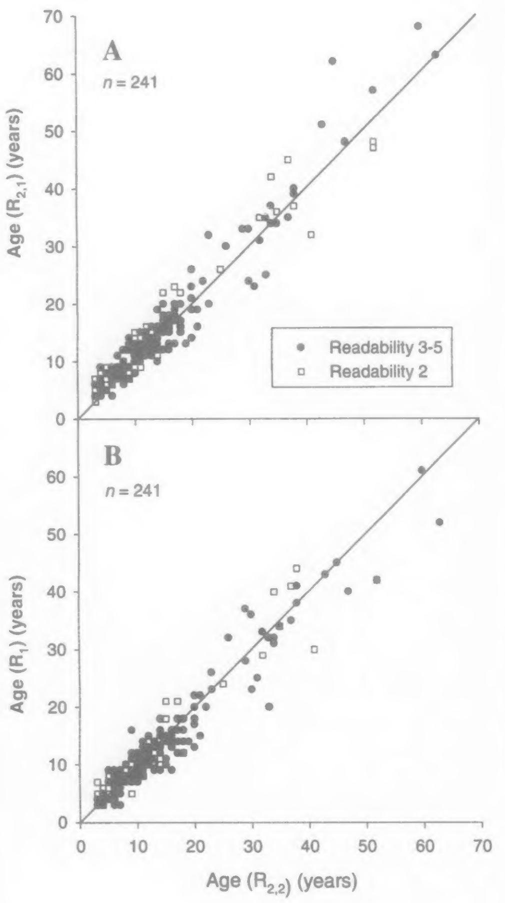

Figure 5

Comparison of hapuku age estimates between (**A**) the two readings of reader 2 ($R_{2,1}$ and $R_{2,2}$), and (**B**) reader 1 (R_1) and reader 2 ($R_{2,2}$). Diagonal lines indicate equality of age estimates.

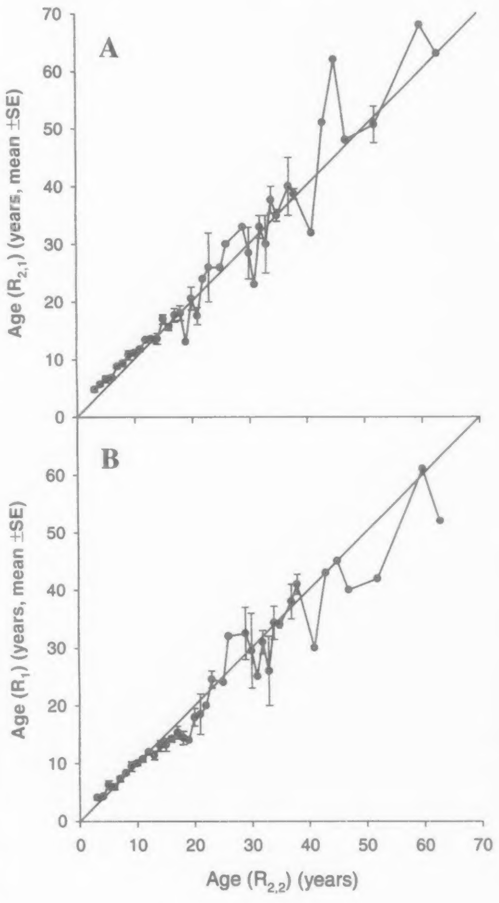

Figure 6

Mean hapuku age estimates of (**A**) reader 2 ($R_{2,1}$), and (**B**) reader 1 (R_1), plotted against the ages determined for the same fish by reader 2 ($R_{2,2}$). The data points are the means and standard errors of the data shown in Figure 5. Diagonal lines indicate equality of age estimates.

sus $R_{2,2}$) (mean=18.0%, range=10.1–26.1%) than between readers (R_1 versus $R_{2,2}$) (mean=21.3%, range=12.6–31.4%). The CV declined slightly with increasing age for both the within- and between-reader comparisons.

The main differences between counts arose from 1) different band counts near the otolith core (potential age difference=1–3 years), 2) different band counts in an unclear central zone around bands 4–8 (several years), and 3) classification of the composition of the otolith margin as opaque or hyaline (one year).

The greatest estimated ages (mean of R_1, $R_{2,1}$ and $R_{2,2}$) were 50.3, 50.7, 59.3, and 63.0 years, but few fish were found to be more than 20 years old (Fig. 5). The youngest hapuku were 3 years old. The von Bertalanffy growth curve fitted to R_1 data differed little from that fitted to $R_{2,2}$ data (Fig. 8A; Table 2). Females grew faster than males, but the difference was slight, and the overlap of data points was substantial (Fig. 8B; Table 2). The largest male was 134 cm, the largest female 147 cm (with three females longer than 140 cm).

Growth curves fitted separately to the northern and central data were very similar (Table 2). Inspection of the residuals from the central curve again

Table 2

Von Bertalanffy growth curve parameters based on hapuku length-at-age and length-frequency data. Standard error estimates for the MULTIFAN parameters are considered unreliable and are not shown. SE = standard error, R_1 = reader 1, $R_{2,2}$ = reading 2 of reader 2, M = male, F = female.

Sample	Otolith reading	Sex	Sample size	$L_\infty \pm$ SE (cm)	$K \pm$ SE	$t_0 \pm$ SE (years)
Length-at-age data (otoliths)						
All	$R_{2,2}$	M + F	241	131.7 ± 3.2	0.0666 ± 0.0059	–4.63 ± 0.72
All	R_1	M + F	241	131.0 ± 2.3	0.0785 ± 0.0052	–2.96 ± 0.48
All	$R_{2,2}$	M	105	129.2 ± 5.4	0.0618 ± 0.0095	–5.75 ± 1.32
All	$R_{2,2}$	F	110	133.2 ± 4.2	0.0698 ± 0.0084	–4.30 ± 1.01
Northern	$R_{2,2}$	M + F	44	124.0 ± 9.8	0.0699 ± 0.0193	–4.51 ± 1.96
Central	$R_{2,2}$	M + F	172	122.6 ± 5.3	0.0794 ± 0.0117	–4.06 ± 0.89
Length-frequency data (MULTIFAN)						
Southern	—	M + F	1,471	549.2	0.0090	–8.02

suggested that females grew slightly faster than males, although there was strong overlap in the ranges (males: mean residual=–1.8 cm, SD=8.6, n=90; females: mean=1.6, SD=7.8, n=82). All growth curves had strongly negative values for t_0 (Table 2).

Length-frequency distributions

Hapuku from the four southern trawl surveys generally were less than 85 cm long (Fig. 9), and because 50% maturity occurs at about 85 cm and 88 cm for males and females, respectively (Johnston, 1983), these would have been immature. The smallest hapuku was 41 cm long, but few fish were less than 50 cm. This reflects the pattern seen in the entire New Zealand research trawl database which contains length measurements for 5841 hapuku: the smallest hapuku was 40 cm, and only 55 were less than 50 cm long.

The best-fit MULTIFAN model consisted of constant length standard deviation with 11 age classes (see Table 2 for growth parameters). The estimated time elapsed between the theoretical birthday and the first appearance of juvenile hapuku in the length-frequency samples (t_1) (based on an estimated minimum age at first capture from otolith ageing of 3 years, plus 0.5 years elapsed between the theoretical birthday [1 September] and the sampling date midpoint [1 March]) was 3.5 years. The age in years since zero length of the youngest age class at the time it first appeared in the length-frequency samples (a_1) was estimated by MULTIFAN to be 11.52 years, producing a t_0 estimate of –8.02 years. The standard error estimates provided by MULTIFAN for the growth parameters are not presented in Table 2 because they tended to be unrealistically small (Francis and Francis, 1992).

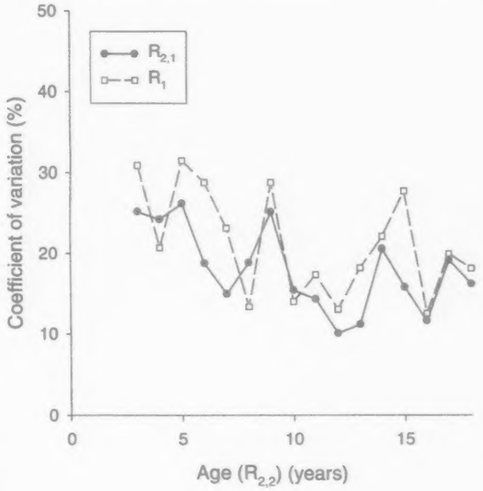

Figure 7

Precision of hapuku age estimates of reader 2 ($R_{2,1}$) and reader 1 (R_1) plotted against the ages determined for the same fish by reader 2 ($R_{2,2}$). The data points are the coefficients of variation of the data shown in Figure 4.

The growth curve resulting from the best MULTIFAN fit to the length-frequency data was nearly linear over the range of the data (Fig. 10). The curve was truncated at 14.5 years, which is the maximum age covered by the data (calculated as the sum of the number of age classes detected by MULTIFAN [11] and the estimated age at first recruitment to the samples [3.5 years]). The MULTIFAN curve should not be extrapolated beyond this point because the

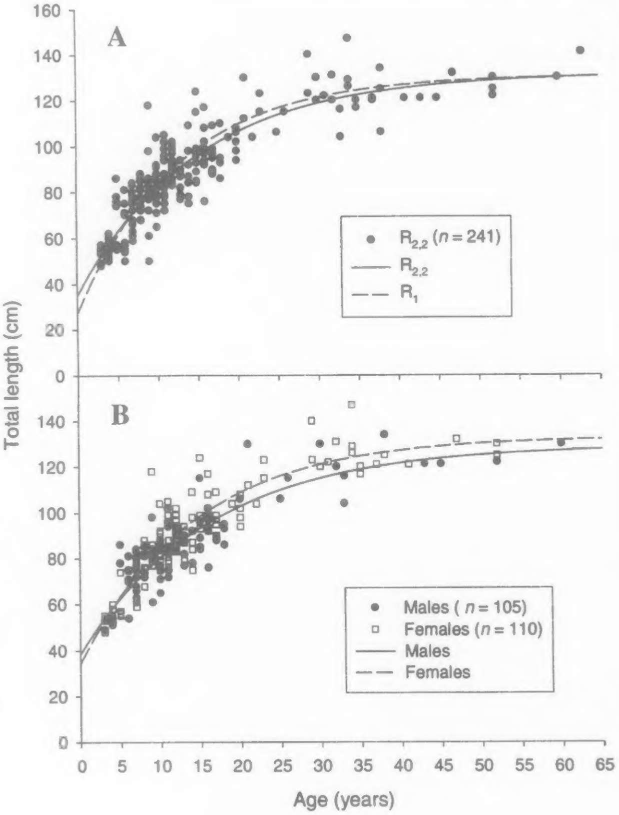

Figure 8

Hapuku length-at-age data ($R_{2,2}$), with fitted von Bertalanffy growth curves for (**A**) all samples and both sexes combined (R_1 and $R_{2,2}$), and (**B**) all samples combined and males and females separately ($R_{2,2}$). See Table 2 for curve equations.

length-frequency data represent only small, immature hapuku. Over the age range 0–12 years, the MULTIFAN growth curve was very similar to growth curves based on otolith ages (Fig. 10).

Tag recapture

One tagged hapuku was recaptured, released with a new tag, and recaptured a second time (Johnston, 1992). It grew from 73 cm to 83 cm during its first 800 days at liberty and from 83 cm to 96 cm during its second 829 days at liberty. This fish was entered into the growth data set three times: once for each of the two periods at liberty and once for the combined period at liberty. All other hapuku used in the growth analysis were recaptured only once.

One hundred and forty four recaptured hapuku had sufficient information (lengths at tagging and recapture, days at liberty) to be used in the growth analysis. Most of these hapuku were between 50 and 90 cm long at tagging (Fig. 11) and would have been immature. The GROTAG reference lengths α and β were set at 55 cm and 85 cm respectively. Periods at liberty ranged from 9 to 3708 days (0–10.2 years), but most fish were at liberty for less than four years (Fig. 12).

Initial GROTAG model fits identified six fish as outliers (fish having absolute standardized residuals greater than 3.0). Five of these fish had negative growth increments of 3–27 cm, and one had a positive increment of 24 cm after 347 days at liberty. These outliers probably resulted from measurement

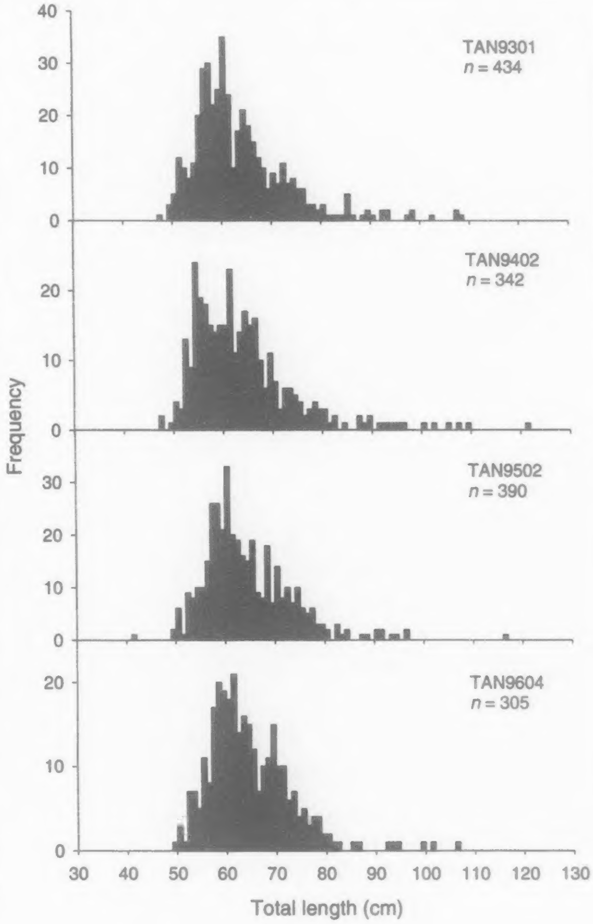

Figure 9

Hapuku length-frequency distributions (both sexes combined) obtained from four *Tangaroa* trawl surveys off Southland in February–March 1993–1996. n = sample size.

errors and were deleted from the data set, leaving 138 fish.

A simple linear model, with a single growth-rate parameter, produced an estimated growth rate of 4.26 cm/yr (Table 3, model 1). A model with two growth-rate parameters produced no improvement in fit (Table 3, model 2). The addition of parameters for outlier contamination, measurement bias, and seasonal growth did not significantly improve the log-likelihood (Table 3, models 3–5), nor did subdivision of the data into three geographical areas (Table 3, model 6). For the Cook Strait data subset, inclusion of separate growth parameters for male and female hapuku did not significantly improve the model fit (Table 4). However, sample sizes were small, statistical power was low, and only large differences could have been detected.

Therefore the best GROTAG model (Table 3; model 1) consisted of simple linear growth over the length range 55–85 cm. It had no apparent pattern or trend in the residuals. GROTAG was then run in simulation mode (Francis, 1988) by using parameter estimates from model 1 to determine the accuracy and precision of the growth-rate estimate. The mean annual growth rate was estimated to be 4.25 cm/yr with a standard error of 0.017 cm/yr.

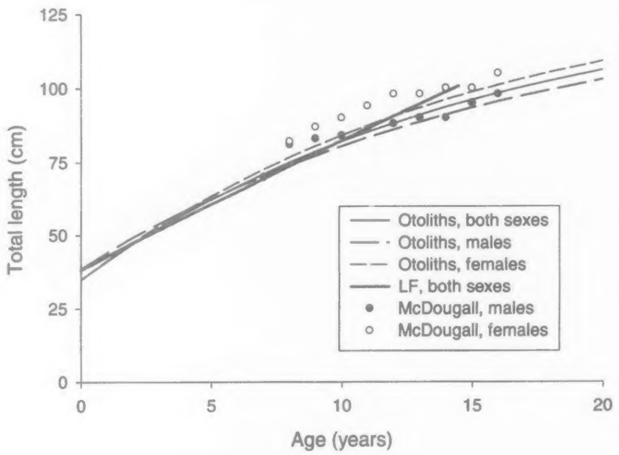

Figure 10

Comparison of growth curves derived from length-at-age data ($R_{2,2}$, otoliths), and MULTIFAN analysis of length-frequency data (LF). Also shown are the mean lengths-at-age reported by McDougall (1975) for hapuku collected in Cook Strait.

Table 3

Parameter estimates from GROTAG growth models for hapuku from all tagging sites (n=138). Seasonal phase is given in years since 1 January. SD = standard deviation; — = parameter not estimated. Models 1–5 are for Poor Knights Islands, Cook Strait, and Oamaru, data combined; model 6 estimated g_{55} separately for the three areas.

		All areas combined					Areas separate
Parameter		1	2	3	4	5	6
Log likelihood	2λ	697.80	697.42	697.80	697.80	694.30	695.85
Mean growth rates	g_{55} (cm/yr)	4.26	4.01	4.24	4.25	4.25	4.1–5.0
	g_{85} (cm/yr)	—	4.38	—	—	—	—
Growth variability	v	0.38	0.39	0.39	0.39	0.39	0.39
SD measurement error	s (cm)	1.55	1.54	1.55	1.55	1.51	1.51
Measurement bias	m (cm)	—	—	—	0.05	—	—
Outlier contamination	p	—	—	0.00	—	—	—
Amplitude	u	—	—	—	—	0.53	—
Phase	w (yr)	—	—	—	—	0.15	—

Discussion

Hapuku otoliths frequently had split opaque bands and were difficult to age. This led to reduced counting precision and, for some age groups, to a small between- and within-reader ageing bias. Our use of marginal increment analysis to validate hapuku otolith ageing was inconclusive. We attribute this to the compound nature of the opaque bands and to the resulting difficulty in determining whether the material being deposited at the margin was opaque or hyaline.

The results of the OTC injection experiment were consistent with the deposition of one opaque and one hyaline band per year. This does not constitute full validation of the otolith ageing technique because the

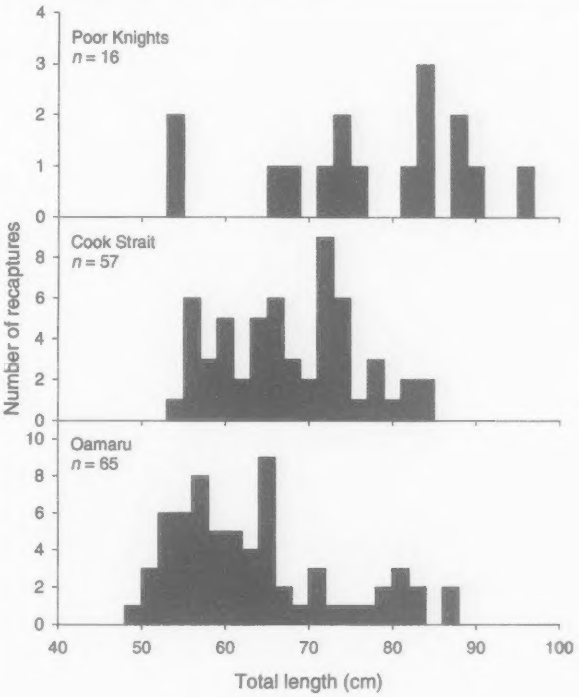

Figure 11

Length-frequency distributions (at tagging) of tagged and recaptured hapuku used in the GROTAG analysis of growth rates. n = sample size.

experiment included only five hapuku, only one of which was at liberty for more than one year. Furthermore, all five fish would have been immature or just maturing at the time of injection. Further validation is required, especially for older, mature hapuku.

An independently derived von Bertalanffy growth curve (based on MULTIFAN analysis of length-frequency data) agreed well with the otolith-based length-at-age curves over the age range 0–12 years but indicated faster growth rates for hapuku aged 12–14.5 years (Fig. 10; Table 5). Our previous experience has shown that MULTIFAN growth curves are generally reliable for younger age classes, which often exhibit discernible length modes, but are not reliable for older age classes, which usually lack any modal length structure. This is because MULTIFAN underestimates the number of older age classes present in the data and consequently overestimates the length-at-age of the older age classes (Francis and Francis, 1992; Francis, 1997). Therefore, the discrepancy between the MULTIFAN and length-at-age curves for the older age classes in Fig. 10 probably arises from bias in the former. This interpretation is supported by the near-linearity of the MULTIFAN growth curve and the implausible MULTIFAN growth parameters, especially L_∞ (Table 2).

Table 4

Parameter estimates from GROTAG growth models for hapuku from Cook Strait (n=43). SD = standard deviation;— = parameter not estimated.

Parameter		Both sexes	Sexes separate M	Sexes separate F
Log likelihood	2λ	240.44	240.26	
Mean growth rates	g_{55} (cm/yr)	4.53	4.44	4.64
	g_{85} (cm/yr)	—	—	
Growth variability	ν	0.27	0.27	
SD measurement error	s (cm)	1.94	1.99	

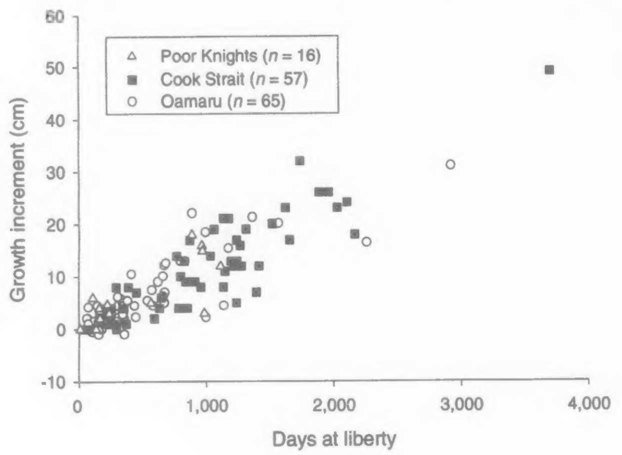

Figure 12

Relationship between growth increment and period at liberty for tagged hapuku. n = sample size.

Table 5

Comparison of hapuku annual growth increments at two reference lengths (55 cm and 85 cm) based on length-at-age ($R_{2,2}$), length-frequency, and tag-recapture data.

Total length (cm)	Annual growth increment (cm)		
	Length-at-age	Length-frequency	Tag-recapture
55	4.94	4.40	4.25
85	3.00	4.15	4.25

The best GROTAG model fit estimated the mean annual growth rate to be 4.25 cm/yr over the length range 55–85 cm. That estimate falls between the length-at-age estimates of annual growth for 55-cm and 85-cm hapuku (Table 5). A nonlinear growth model was not significantly better than the linear model, probably because of the narrow length range of the tag-recapture data, and the small sample size (n=138).

We conclude that the growth curves and growth rate estimates derived from length-frequency and tag-recapture data are consistent with those from otolith-based, length-at-age data for the length and age ranges over which the data overlap. In conjunction with the results of the OTC injection experiment, this agreement among growth-rate estimates provides strong support for our hypothesis that otolith band pairs are deposited annually in hapuku.

Our length-at-age growth curve for male hapuku is similar to that of McDougall (1975), who made band counts in broken and burnt otoliths from hapuku collected in Cook Strait (Fig. 10). However, McDougall reported a slightly faster growth rate for females (Fig. 10). It is not possible to determine whether the difference in female growth rates is real, or a result of McDougall's small sample size (n=72). McDougall's largest hapuku was 120 cm and his oldest fish was 26 years.

A study of hapuku growth at Juan Fernández Island, based on scale annuli, reported much faster growth rates and a maximum age of only 12 years (Pavez and Oyarzún, 1985). Scale rings are typically crowded to the point of being unresolvable in hapuku older than 8 years (McDougall, 1975); it is likely therefore that the ages of Pavez and Oyarzún's larger fish were underestimated.

Lack of precision and reader bias mean that otolith ageing is unlikely to be useful when accurate hapuku ages are required (e.g. in the estimation of year-class strength from an age-frequency distribution). However, the precision and accuracy problems experienced in this study had little effect on the shape of growth curves fitted to length-at-age data, and we believe that the growth parameters reported here are relatively robust.

The large negative t_0 values for all growth curves indicate a lack of fit of the von Bertalanffy model to the data for small hapuku. This may result from one or more of the following: 1) lack of fish less than three years old in our data; 2) underestimation of the ages of hapuku because of failure to recognize and count all the annual bands near the core; or 3) different growth rates of pelagic juveniles, and demersal juveniles and adults. Interestingly, Pavez and Oyarzún's (1985) scaled-based growth curves had t_0 values close to zero, and estimated ages at the length of settlement similar to ours (i.e. 38 cm at age 3 and 49 cm at age 4). Scale bands may therefore help to resolve problems experienced in interpreting otolith cores when ageing small hapuku.

Small juvenile hapuku pass through a pelagic stage in surface waters, usually associated with flotsam, and are rarely caught (Cormack, 1986; Michael, 1988; Roberts, 1996). At the end of the pelagic stage, they become demersal in depths of 50–600 m. Bottom trawl length-frequency data (Fig. 9; NIWA[2]) and bottom set-net and line records (Johnston, 1983; Roberts, 1989) indicate that most hapuku switch from a pelagic to demersal life style at around 50 cm, although hapuku as small as 40 cm have been caught by bottom trawl. A 35-cm hapuku reported caught in Wellington Harbour by Hector (1888) may have been a pelagic juvenile, but no details were given of habitat or fishing method. A small number of pelagic juveniles up to 67 cm long have been caught on surface longlines over 2000 m or more of water (Roberts, 1996; Scientific Observer Database[3]). These large pelagic juveniles may have become "stranded" in the pelagic environment after being carried over deep water by oceanic currents. Presumably they remain in surface waters until they encounter shallower depths, at which time they settle to the seabed.

Our best estimate of the age at which hapuku settle to a demersal habitat is 3–4 years, but our interpretation of the banding pattern near the otolith core was uncertain and somewhat subjective. Counts of possible daily increments in otolith sections also suggest settlement at about 3 years (Roberts, 1996), and a similar age range has been suggested by other studies (McDougall, 1975; Johnston, 1983). *Polyprion americanus* apparently settles at lengths greater than 45–55 cm and ages greater than 1–7 years (Sedberry et al., 1996).

The age at recruitment of hapuku to commercial trawl catches is likely to be the same as the age at settlement to the seabed. Although our research vessel samples were caught with a small mesh (60-mm) codend, hapuku longer than 50 cm are also retained by the larger mesh sizes used by commercial vessels (typically 100–125 mm) (Hurst and Bagley, 1997).

Previous studies have suggested that female hapuku grow larger and faster than male hapuku (McDougall, 1975; Roberts, 1986; 1989). Our results support those conclusions but also indicate that the differences in both maximum length and growth rate are small and, for most purposes, trivial. However, our ability to detect growth rate differences between the two sexes, and between sample sites, was limited by the low precision of our age estimates and the small sample sizes available for the GROTAG analysis.

Hapuku mature at about 85 and 88 cm, males and females, respectively (Johnston, 1983). Based on the length-at-age growth curves given in Table 2, age at maturity is estimated to be 10–13 years for both sexes.

The largest hapuku in our study was 147 cm TL, but they are known to reach 178 cm TL and 76 kg in weight (Roberts[4]). The longevity of hapuku cannot be precisely determined because of difficulties we experienced in estimating ages from otoliths, and because our samples mostly came from populations of hapuku that had been exploited for many years. Our study does suggest that hapuku live at least 50 years, possibly in excess of 60 years.

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An analysis of the possible utility of time–area closures to minimize billfish bycatch by U.S. pelagic longlines

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Abstract.–This study examined the relative rates of billfish bycatch and target species catch by areas (1°, 2°, and 5° latitude and longitude) and months in the catch data reported in mandatory log books kept by U.S. pelagic-longline fishermen in order to identify potential time–area strata that could reduce billfish bycatch. The 1986–91 mean percentages identified month–area strata with high percentages of sailfish and marlin bycatch and marlin only bycatch. The analyses indicated that the elimination of effort in cells selected according to percentages of billfish in the catch could have reduced the 1986–91 billfish bycatch by 50% and the target species from 13.9 to 19.2%, depending on the spatial resolution employed. The corresponding analysis of marlin only indicated a 50% reduction in marlin bycatch could have been attained and a 16.4–20.7% reduction in the target species catch. The time–area closures identified in the 1986–91 logbook data were applied to the data for 1992–95 and provided a test of the spatial and temporal stabilities of these results. For the evaluation of sailfish and marlin combined, the reductions in both billfish bycatch and target species catches averaged less than the predicted values, but in all cases billfish were selectively protected. For the evaluation of marlin only, the reduction of sailfish bycatch was less than the predicted amount and the reduction of the target species was slightly greater than the predicted value. The agreement between the predicted level of protection for billfish or marlin and the mean value for the 1992–95 test period increased with increasing size of the grid. At the 5°cell size, the mean reduction was 22.8% for the targeted species and 48.6% for marlin (compared with predicted values of 20.7 and 50% respectively). These results suggest that time and area restrictions on fishing could significantly reduce the bycatch of billfishes in the pelagic-longline fisheries without equivalent reductions in the catch of target species.

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The U.S. Fisheries Management Plan for Atlantic Billfishes (sailfish, blue and white marlin, and spearfish) reserves billfish stocks for recreational use; their commercial harvest by U.S. fishermen has been prohibited since the plan became effective in 1988 (SAFMC, 1988). The most recent stock assessment for billfishes found that, over the Atlantic as a whole, blue and white marlin stocks are seriously overfished (Anonymous, 1996). Their stocks were at about 21 and 24%, respectively, of the biomass needed to support maximum sustainable yield (MSY) at the beginning of 1996 (Anonymous, 1996). Fishing-induced mortality was estimated to be 3.19 times higher than that which would produce MSY for blue marlin, and 1.88 times higher than that which would produce MSY for white marlin. Most of the fishing mortality on these species is the result of bycatch in the pelagic-longline fisheries that target other species, particularly tuna and swordfish.

Many authors have promoted the concept of marine reserves (also called marine protected areas or MPAs) as management tools to enhance conservation of fishery resources (Bohnsack, 1994; Shackell and Wilson, 1995; Hutchings, 1995, 1996; Allison et al., 1998; Lauck et al., 1998). Closed areas have been used in many parts of the world to control bycatch mortality (Alverson et al., 1994). Hutchings (1996) noted that MPAs might have considerable merit in reducing bycatch when assessed against the effectiveness of other forms of regulatory control such as bycatch limitations and catch quotas. Often, however, the concept of marine reserves is restricted to closures of particular habitats or portions of habitats. Kenchington (1990) noted that such marine reserves would be of little use for species such as billfish that have both pelagic larvae and highly pelagic adults. Among other options for reducing bycatch, Alverson et al. (1994) observed that time–area control of fishing activity offers an opportunity to reduce unwanted bycatch. The main objective of employing time–area strategies is to take advantage of variation in the degree of co-occurrence between target and bycatch species (Murawski, 1992). The effectiveness of such controls obviously depends on the degree of overlap between the bycatch and the targeted species (Adlerstein and Trumble, 1992).

Cramer (1996) used logbook data on U.S. large pelagic fish (data that have been mandatory since October 1986) in order to evaluate the spatial distribution of the catch of undersized swordfish by the longline fishery in strata of 1° latitude and longitude by season and area. Her study evaluated the implications of removing time–area strata with high swordfish discard rates on the total catch of the longline fishery. The present study uses the same data set to evaluate the degree of overlap between billfish bycatch and target species catch for the U.S. pelagic longline fishery and develops a method for selecting candidate time–area cells whose closure would selectively enhance billfish survival and minimize impacts on the target species catch.

Methods

The longline catch data were inspected 1) to determine the species composition of the catch to identify the set of species which, taken together, constitute the primary targets of the fishery, and 2) to identify possible trends in the reporting of billfish bycatch. The reported bycatch of billfish declined markedly in 1992 compared with earlier years. Consequently, the data were partitioned into two periods: 1986–91 and 1992–95. Data from the first period were used to characterize the spatial and temporal distributions of the catch. Data from the second period were used to test temporal stability of the results of analyses of the first period.

The billfish bycatch and the combined billfish (sailfish, spearfish, and blue and white marlin) bycatch as well as the target species catch for each longline set of each reported trip were summed into cells of 1°, 2°, and 5° latitude and longitude and month over the period 1986–91. The analysis was also repeated and only blue and white marlin bycatch was considered along with the target catch. Separate cumulative frequency distributions of the percentage of billfish or marlin bycatch in the combined billfish and target species catches by number by cell were constructed for each level of spatial resolution. These frequency distributions were used to estimate the percent reduction in billfish bycatch and target species catch that would have occurred if the effort in time–area cells with billfish or marlin bycatch rates above an arbitrary threshold had been completely eliminated during the 1986–91 fishery. The distribution of the minimum number of cells producing any specific reduction in billfish or marlin catches with the least impact on target species catch could then be determined from these data.

As an example, the distribution of cells that, if they had been eliminated from the 1986–91 U.S. fishery, would have reduced the billfish and marlin bycatches by 50%, were plotted for examination. Although the reporting rate declined after 1991, the temporal and spatial relative distributions of billfish in the total longline catch would be unaffected, so long as the change in the reporting rate was random. Consequently, the temporal stability of the reduction in billfish and marlin bycatch for the time–area cells identified with the 1986–91 data was evaluated by using data from 1992 to 1995. This was done by calculating the percent reduction in the total billfish and marlin bycatch that would have occurred each year if the time–area cells identified in the 1986–91 data had been closed. This analysis assumed that the displaced effort would not shift elsewhere.

Results

The catch by species in the data file from U.S. pelagic longline logbooks from 1986 through 1995 is presented in Table 1. Inspection of these data indicates that the predominant target species of this fishery included swordfish, yellowfin tuna, bigeye tuna, albacore, and dolphin fish. Together they constituted 90% of the nonbillfish harvest that was reported in these logbooks. For this analysis, billfish bycatch is the combined catch of sailfish, spearfish, and blue and white marlin, and marlin bycatch is the combined catch of blue and white marlin. Inspection of the data in Table 1 indicates a sharp drop in the numbers of billfish caught after 1991. This is possibly a consequence of a change in reporting trends following the U.S. billfish management plan's prohibition of the sale of billfish, or the restrictions on landing undersized swordfish imposed in mid-1991, rather than a consequence of a true reduction in the bycatches of billfish by the U.S. pelagic-longline fleet. Although no observer data are available before 1992, this conclusion is supported by data collected by observers on longline vessels that indicate billfish bycatch rates after 1992 were much higher than those reported in the logbooks (Cramer[1]). For this reason, the longline logbook data were grouped into two periods: 1986–91 and 1992–95. Data from 1986 through 1991 were used to characterize the distribution of billfish and target species catches, and data from 1992 through 1995 were used to test the spatial and temporal stability of the patterns observed in the 1986–91 data.

The percentage of billfish in the combined billfish bycatch and target species catch for each month–area cell in strata of 1°, 2°, and 5° was estimated, and the results were sorted to obtain cumulative frequency distributions of the billfish bycatch percentages for each spatial resolution. At the same time, the cumulative catches of billfish and target species were compiled for each observation in the cumulative frequency distributions of percentage of billfish in the catch in each time–area cell. The results of this procedure are presented in Figure 1 and Table 2. Note

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[1] Cramer, J. 1996. Pelagic longline billfish bycatch. International Commission for the Conservation of Atlantic Tunas (ICCAT) working document SCRS/96/97.

Table 1

Catch in number (not including billfish discards) by species reported in the logbook data for U.S. pelagic longlines for 1986–95.

Species	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Total
Swordfish	16,510	113,665	161,980	171,344	129,147	86,586	67,004	64,724	63,913	72,520	947,393
Bluefin tuna	58	484	422	717	599	540	1010	342	335	266	4773
Albacore	1181	2085	2984	3986	8220	9873	14,137	13,636	18,795	21,810	96,707
Bigeye tuna	3162	15,919	15,249	19,764	16,947	18,250	15,239	21,446	22,859	25,363	174,198
Yellowfin tuna	9241	59,665	67,569	83,844	68,711	70,433	94,510	68,360	73,337	85,135	680,805
Blackfin tuna	64	560	808	1450	1090	1525	3178	2797	3096	2363	16,931
Skipjack tuna	0	0	0	0	0	1384	2165	1374	232	279	5434
Bonito	0	0	0	0	0	0	0	238	1030	497	1765
Other tuna	0	0	0	0	0	0	1695	613	337	451	3096
Blue marlin	115	815	387	65	82	55	3	64	62	23	1671
Sailfish	4	55	147	53	66	22	5	34	56	87	529
Spearfish	4	52	47	2	15	2	8	30	19	14	193
White marlin	217	998	468	97	48	62	13	36	27	20	1986
Greater amberjack	0	0	0	0	0	0	112	836	1278	234	2460
Banded rudderfish	0	0	0	0	0	0	3	13	29	86	131
Dolphin fish	972	7861	10,768	29,899	31,899	32,576	25,351	26,142	29,617	72,321	267,406
King mackerel	1	11	35	119	11	67	118	4602	7176	1929	14,069
Wahoo	40	1346	2629	3157	3560	3736	6506	4393	3442	5477	34,286
Oilfish	0	0	0	0	0	0	0	37	5073	5102	10,212
Blue shark	944	1482	581	980	633	753	2050	1513	864	373	10,173
Mako shark	486	4055	4877	6946	4380	3475	414	338	371	187	25,529
Shortfin mako shark	0	0	0	0	0	0	3944	3738	3982	3747	15,411
Oceanic whitetip shark	0	0	0	0	0	0	319	226	166	205	916
Porbeagle shark	0	0	0	0	0	0	41	675	1591	509	2816
Bigeye thresher shark	0	0	0	0	0	0	200	304	626	472	1602
Other pelagic shark	0	0	0	0	0	0	0	0	0	8	8
Thresher shark	32	674	632	488	280	194	113	139	95	181	2828
Dusky shark	0	0	0	0	0	0	3365	7305	2826	2830	16,326
Bignose shark	0	0	0	0	0	0	70	254	124	123	571
Blacktip shark	0	0	0	0	0	0	3527	5965	6042	3954	19,488
Hammerhead shark	57	129	535	979	500	262	360	562	508	349	4241
Scalloped hammerhead shark	0	0	0	0	0	0	292	267	646	375	1580
Smooth hammerhead shark	0	0	0	0	0	0	627	452	484	231	1794
Night shark	0	0	0	0	0	0	478	455	379	421	1733
Silky shark	0	0	0	0	0	0	1685	1244	2134	2765	7828
Spinner shark	0	0	0	0	0	0	925	255	234	209	1623
Tiger shark	27	104	1051	183	98	108	165	173	477	202	2588
Other sharks	842	5740	4380	5424	9750	4620	3242	4242	1092	1376	40,708
White shark	20	137	1723	1222	537	95	104	163	16	2	4019
Sandbar shark	0	0	0	0	0	0	0	0	2020	14,192	16,212
Other	0	0	0	0	0	0	0	0	90	2515	2605

that the initial slope of the relation between the billfish percent reduction and target species percent reduction is much lower than 1.0 for each of the spatial resolutions examined. This finding suggests that the temporal and spatial distributions of billfish bycatch and target species are somewhat different and that it should be possible to selectively reduce the longline billfish bycatch in relation to target species catch. The data from Table 2 indicate that a 10% reduction in the 1986–91 billfish bycatch could have

Table 2

Estimated reduction in billfish bycatch and target species catch by elimination of time–area cells where the billfish percentage of catch is greater than or equal to the specified threshold value based on 1986–1991 catch rates in the U.S. pelagic-longline fishery. These estimates assume that the displaced effort will not be redirected elsewhere.

	1° cells		2° cells		5° cells	
Billfish reduction (%)	Threshold (%)	Target reduction (%)	Threshold (%)	Target reduction (%)	Threshold (%)	Target reduction (%)
5	18.46	0.34	14.23	0.49	9.64	0.94
10	14.32	1.01	9.99	1.51	8.77	2.33
15	12.06	1.90	9.44	2.73	7.94	3.88
20	10.07	2.97	8.52	4.08	7.58	5.52
25	8.81	4.25	7.17	5.62	7.34	7.21
30	7.52	5.74	5.86	7.54	6.10	9.19
35	6.78	7.45	5.47	9.70	5.70	11.38
40	6.16	9.37	4.87	12.13	5.52	13.68
45	5.49	11.49	4.61	14.77	4.86	16.29
50	4.95	13.87	4.32	17.57	4.36	19.17
55	4.37	16.59	4.10	20.53	4.21	22.28
60	4.03	19.59	3.79	23.72	3.95	25.51
65	3.61	22.85	3.51	27.16	3.57	29.11
70	3.30	26.53	3.21	30.92	3.11	33.13
75	2.94	30.62	2.95	35.01	2.76	37.67
80	2.56	35.30	2.48	39.73	2.46	42.92
85	2.17	40.73	2.19	45.21	2.07	48.85
90	1.74	47.38	1.70	52.09	1.73	55.91
95	1.20	56.08	1.15	61.54	1.26	65.08

been attained with only a 1 to 2.3% reduction in the catch of target species, depending on the spatial resolution employed. This reduction would have been achieved by eliminating the effort in months and areas where the reported billfish bycatch exceeded the threshold percentage of billfish in the combined catch in Table 2. Similarly, a 50% reduction in the 1986–91 billfish bycatch would have been achieved by eliminating the effort in cells where the reported billfish bycatch exceeded the table values with corresponding reductions of 13.9 to 19.2% in the harvest of target species. A 95% reduction in the 1986–91 billfish bycatch would have been achieved by eliminating all effort in cells with reported catches of more than 1.2, 1.15, or 1.26% billfish for 1°, 2°, or 5° cells, and there would have been a concomitant reduction in target species catch of 56.1, 61.5, or 65.1%, respectively.

The same type of analysis was conducted with only blue and white marlin as the billfish species of concern. The results are presented in Figure 2 and Table 3. As with billfish combined, the initial slope of the relation between the percent catch of marlin bycatch and of target species is much less than 1.0. This result also indicates that the combined marlin bycatch can be reduced by the elimination of select time–area strata and that the catch of target species would not be proportionately affected. The data from Table 3 indicate that a 10%

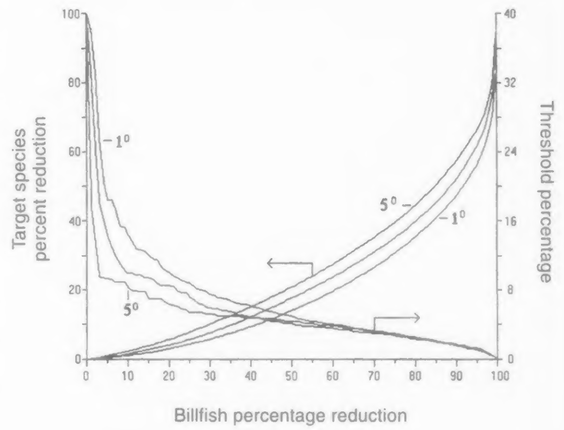

Figure 1

Percent reduction in target species and marlin bycatch associated with the removal of effort in time–area cells above the indicated threshold percentage of all billfish in the catch for cell sizes of 1°, 2°, and 5° of latitude and longitude.

Table 3

Estimated reduction in blue and white marlin bycatch and target species catch by elimination of time–area cells where the marlin percentage of catch is greater than or equal to the specified threshold value based on 1986–91 catch rates in the U.S. pelagic-longline fishery. These estimates assume that the displaced effort will not be redirected elsewhere.

	1° cells		2° cells		5°cells	
Marlin reduction (%)	Threshold (%)	Target reduction (%)	Threshold (%)	Target reduction (%)	Threshold (%)	Target reduction (%)
5	18.15	0.38	11.54	0.53	7.32	1.11
10	10.16	1.14	7.06	1.71	6.22	2.79
15	7.71	2.34	5.19	3.50	5.49	4.76
20	6.17	3.79	4.79	5.37	5.21	6.33
25	5.77	5.10	4.24	7.44	4.83	8.62
30	4.97	6.80	4.02	8.99	4.65	10.81
35	4.54	8.57	3.87	11.59	4.16	13.63
40	4.15	10.95	3.64	14.14	4.02	15.70
45	3.78	13.60	3.44	16.55	3.86	17.72
50	3.46	16.37	3.23	19.55	3.58	20.74
55	3.24	19.50	3.12	22.44	3.12	23.66
60	3.00	22.03	2.87	25.95	2.84	27.44
65	2.76	25.04	2.67	29.47	2.68	30.54
70	2.39	28.50	2.39	32.87	2.47	34.89
75	2.14	32.94	2.10	36.53	2.20	38.76
80	1.86	37.90	1.85	41.40	2.01	44.08
85	1.56	43.97	1.67	46.43	1.78	49.78
90	1.21	50.49	1.23	53.72	1.49	56.75
95	0.73	59.39	0.84	63.06	1.07	66.45

reduction in the 1986–91 marlin bycatch could have been attained with only a 1.1 to 2.8% reduction in the catch of target species, depending on the spatial resolution employed. This would result by eliminating the effort in months and areas where the reported billfish bycatch exceeded the threshold percentage of billfish in the combined catch indicated in Table 3. Similarly, a 50% reduction in the 1986–91 marlin bycatch would have been obtained by eliminating the effort in cells where the reported billfish bycatch exceeded the table values with corresponding reductions of 16.4 to 20.7% in the harvest of target species. A 95% reduction in the 1986–91 marlin bycatch would have been achieved by eliminating all effort in cells that reported catches of more than 0.73, 0.84, or 1.07% marlin for 1°, 2°, or 5° cells, and there would have a concomitant reduction in target species catch of 59.4, 63.1, or 66.5% respectively.

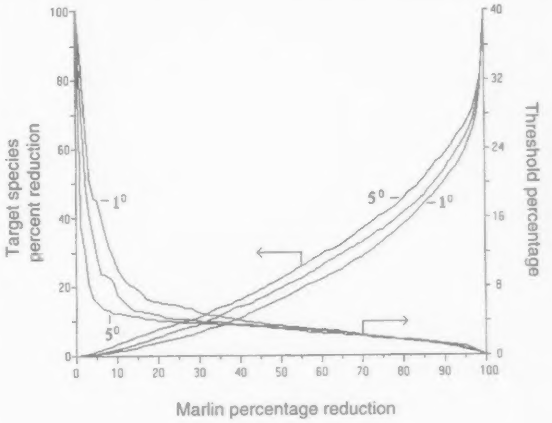

Figure 2

Percent reduction in target species and blue and white marlin bycatch associated with the removal of effort in time–area cells above the indicated threshold percentage of marlin in the catch for cell sizes of 1°, 2°, and 5° of latitude and longitude.

Obviously, the temporal and spatial distribution of the cells that would be eliminated with the current method for any particular threshold selected is of considerable interest. Figure 3 presents the distribution of cells by area and month that correspond to a threshold selection that would have eliminated 50% of the billfish bycatch from the 1986–91 U.S. pelagic-longline fishery as reported in the log books. Areas where fishing effort was expended within 5° cells are stippled or diagonally

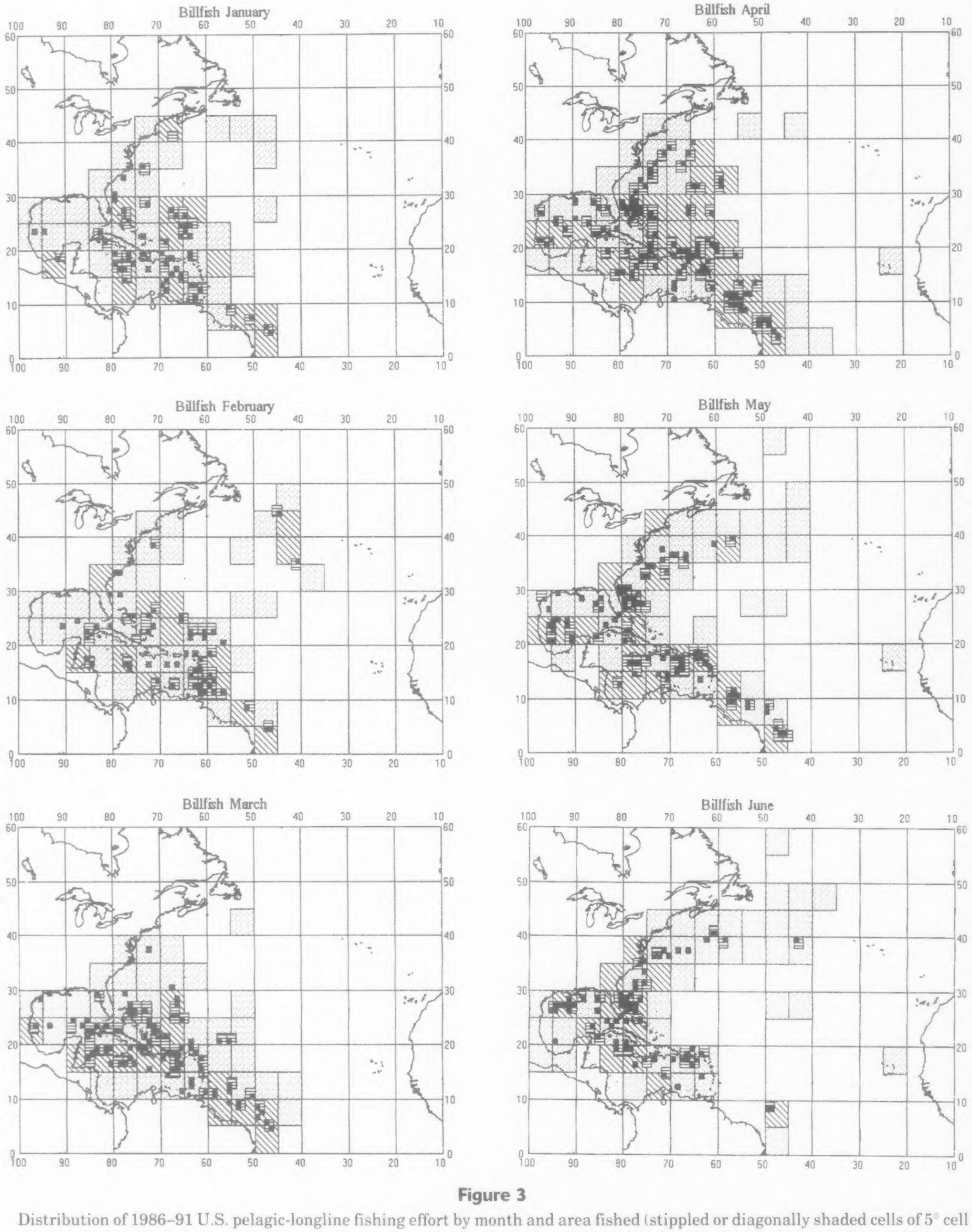
Billfish January
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Figure 3

Distribution of 1986–91 U.S. pelagic-longline fishing effort by month and area fished (stippled or diagonally shaded cells of 5° cell or smaller. Month–area cells where billfish bycatch percentages were greater than the 50% threshold levels for 1° (filled), 2° (horizontal shading) and 5° (diagonal shading) cells. Elimination of the effort in these cells would have reduced the combined billfish bycatch by 50% and reduced the target species catch by 13.9, 17.6, and 19.2% respectively.

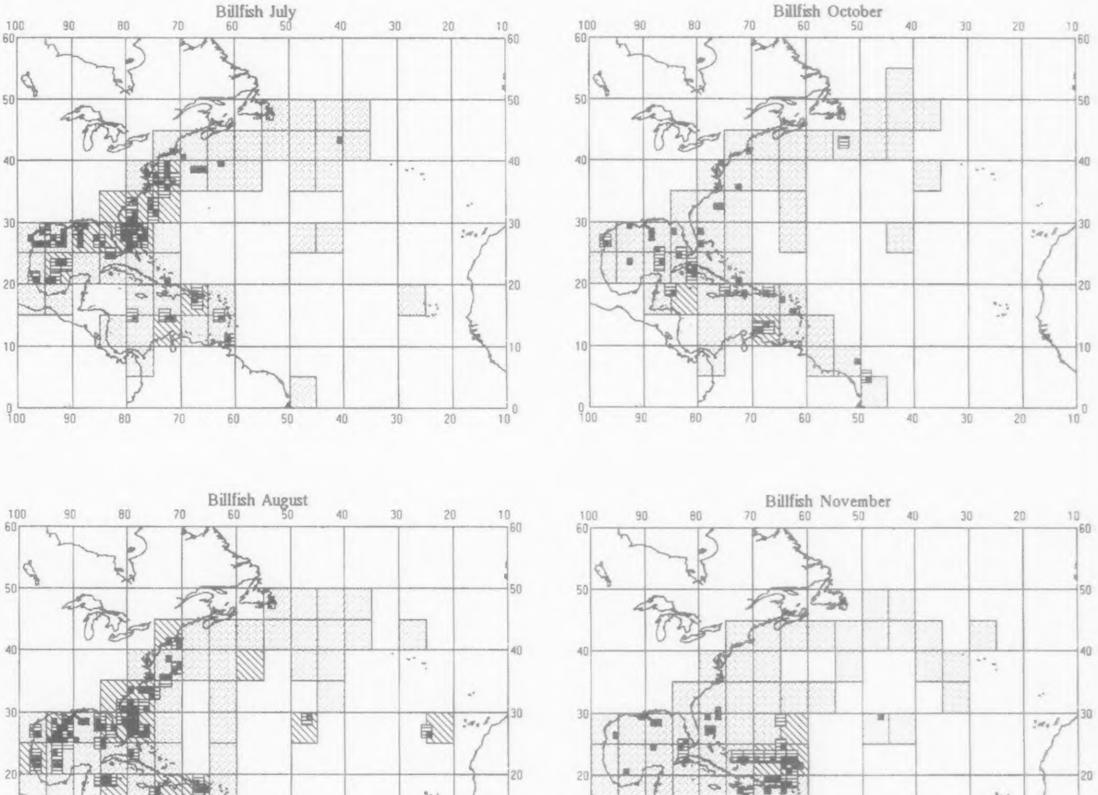
Billfish July
Billfish October
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Figure 3 (continued)

shaded. The diagonally shaded 5° cells indicate where the billfish proportion of the catch within the 5° area exceeded the 4.36% threshold required to obtain a 50% reduction in the 1986–91 billfish bycatch indicated in Table 2. The horizontally shaded 2° cells indicate those cells where the billfish proportion exceeded the threshold for the 2° spatial resolution, and the filled 1° cells indicate those cells where the billfish proportion exceeded the 1° threshold. Inspection of these plots indicates a temporal pattern in the distribution of fishing effort—from southern waters in the winter to northern and eastern waters during the summer and fall. Also the minimum number of cells that would have to have been eliminated from the 1986–91 fishery to reduce the billfish bycatch by 50% occur during the months of September through November. There is also a tendency for the affected cells to move north from the southernmost regions fished in November and December to the entire U.S. coastline by July and August.

Similar plots are presented for marlins in Figure 4, with the respective threshold percentages of marlin in the catch. As for billfishes combined, the number of cells above the threshold percentages is at a minimum in October but increases thereafter to a peak in April. The affected cells move north during the spring and summer from primarily southern latitudes in the winter. However, some cells in the Caribbean exceed the 50% thresholds of Table 3 in almost every month.

To test the temporal and spatial stability of the areas identified in Figures 3 and 4, I calculated the percent reductions in billfish and marlin bycatch and target species that would have occurred if those areas had been closed in each year from 1992 through 1995 for each level of spatial resolution considered (Tables 4 and 5). These estimates assumed that the time–area strata identified for closure would not be redirected elsewhere but did include strata fished in 1992–1995 that were not present in the 1986–91 base period. For billfish combined, billfish would have been selectively protected by closing the time–area cells identified from the 1986–91 data evaluation each year from 1992 through 1995 with all levels of spatial resolution examined. The agreement between predicted and 1992–95 observed values increased with increasing grid size (Table 4). Mean billfish reductions increased from 28.6% to 41.6% from 1° to 5° cells compared with the predicted levels of 50%. The mean reductions for targeted species were slightly less than the predicted values. The observed mean values were 12.8, 11.9, and 16.7%, compared with the predicted values of 13.9, 17.6, and 19.2% for the 1°, 2° and 5° cells, respectively. In general, the larger 5° grid produced results that were closest to the values predicted from the 1986–91 data set and showed the least year-to-year variability in the percent reduction of billfish bycatches.

For the analyses considering marlin species only, marlins would also have been selectively protected by closing the time–area cells identified from the 1986–91 data evaluation each year from 1992 through 1995 with all levels of spatial resolution examined. The agreement between predicted and 1992–95 observed values also increased with increasing grid size (Table 5) but were closer to the predicted values than for the evaluation of billfish combined. Mean marlin reductions increased from 35.7% to

Table 4

Evaluation of the temporal stability of the estimated percentage changes in billfish bycatches and target species catches using the time–area closures identified in the analyses of the 1986–91 longline data. The threshold levels were selected to reduce combined billfish bycatch by 50%, and the time–area cells that were excluded are those indicated in Figure 3. The estimated percentage reductions are based on the proportion of the annual total catch within the cells identified for closure and include areas fished in 1992–95 that had not been fished during the 1986–91 base period. The columns labeled "cells" are the percentages of the time–area strata fished during the year that would have been eliminated by closing the indicated cells.

	Predicted percentage reduction with billfish threshold model								
	1° cells			2° cells			5° cells		
Year	Billfish	Target	Cell	Billfish	Target	Cell	Billfish	Target	Cell
1992	24.5	11.7	15.7	25.8	10.7	14.1	42.2	15.7	20.3
1993	37.0	15.5	16.1	33.7	13.2	13.2	39.1	17.9	19.3
1994	32.1	13.6	19.1	35.5	12.7	14.7	44.5	17.8	20.7
1995	20.8	10.2	13.7	23.2	10.9	14.5	40.7	15.2	19.9
Mean	28.6	12.8	16.2	29.6	11.9	14.1	41.6	16.7	20.1

48.6% from 1° to 5° cells compared with the predicted levels of 50%. The mean reductions for targeted species were slightly greater than the predicted values. The observed mean values were 18.6, 20.1, and 22.8%, compared with the predicted values of 16.4, 19.6, and 20.7% for the 1°, 2° and 5° cells, respectively. As with billfish combined, the larger 5° grid produced results that were closest to the values predicted from the 1986–91 data set and showed the least year-to-year variability in the percent reduction of marlin catches. Overall, the result for marlin at the 5° resolution was in remarkable agreement with the values predicted from the evaluation of the 1986–91 data.

Discussion

This study was intended to consider pelagic longlines only. However, bottom-longline and pelagic-longline sets could not always be clearly distinguished in the database used for the analysis. Consequently, some of the effort and catch included in the analyses were likely from bottom-longline sets. Some additional refinement of the analyses might have been possible with additional attention to eliminating bottom-longline data. However, the total of the bottom-longline sets is thought to be only about 10% of the longline sets in the database (Cramer[2]), and all identified bottom-longline sets were eliminated from the analysis. Consequently, it is not likely that a complete elimination of the bottom-longline sets would have had an important effect on the basic pattern seen in the results of this study.

The International Commission for the Conservation of Atlantic Tunas (ICCAT) CPUE data files (task ii) indicate that billfish often accounted for 15% or more of the Japanese longline catch in the Gulf of Mexico and Caribbean before about 1977. However, the total harvest of billfish by the pelagic-longline fishery documented in the 1986–95 U.S. logbooks was never large in comparison with other species in their reported catch, and most were discarded even before the prohibition on harvest was promulgated by the U.S. Atlantic Billfish Plan. According to logbook records only 16.26% of the billfish caught during the period 1986–89 were retained. This figure dropped to 4.82% for the period 1992–95. Observer data for pelagic-longline trips indicate that the actual bycatch rates for billfish in this fishery are much higher than is currently being reported in logbooks (Cramer[1]). This phenomenon perhaps exists because billfish are not economically important components of the harvest, a phenomenon that was intensified by the U.S. Atlantic Billfish Plan which prohibited commercial harvest of billfishes after 1988. If so, it is likely that billfish were under-reported in the logbook data for the 1986–91 period used in the present analysis. The magnitude of the reporting rate is unknown for the 1986–91 period. However, unreported rates would not pose a problem for the analysis presented here if they were randomly distributed in time and space. This question could possibly be addressed in future analyses by using observer data from U.S. domestic pe-

Table 5

Evaluation of the temporal stability of the estimated percentage changes in marlin and target species catches using the time–area closures identified in the analyses of the 1986–91 longline data. The threshold levels were selected to reduce marlin catch by 50%, and the time–area cells that were excluded are those indicated in Figure 4. The estimated percentage reductions are based on the proportion of the annual total catch within the cells identified for closure and include areas fished in 1992–95 that had not been fished during the 1986–91 base period. The columns labeled "cells" are the percentages of the time–area strata fished during the year which would have been eliminated by closing the indicated cells.

	Predicted percentage reduction with marlin threshold model								
	1° cells			2° cells			5° cells		
Year	Marlin	Target	Cell	Marlin	Target	Cell	Marlin	Target	Cell
92	24.7	15.0	17.8	41.0	18.2	19.7	48.9	20.4	23.3
93	38.3	19.8	18.6	43.8	20.8	17.8	45.3	22.7	19.8
94	44.9	21.5	20.5	47.0	20.4	17.3	47.6	23.1	23.2
95	35.0	18.2	16.2	45.8	21.1	18.2	52.5	24.9	22.7
Mean	35.7	18.6	18.3	44.4	20.1	18.3	48.6	22.8	22.2

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[2] Cramer, J. 1996. Sustainable Fisheries Division, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149.

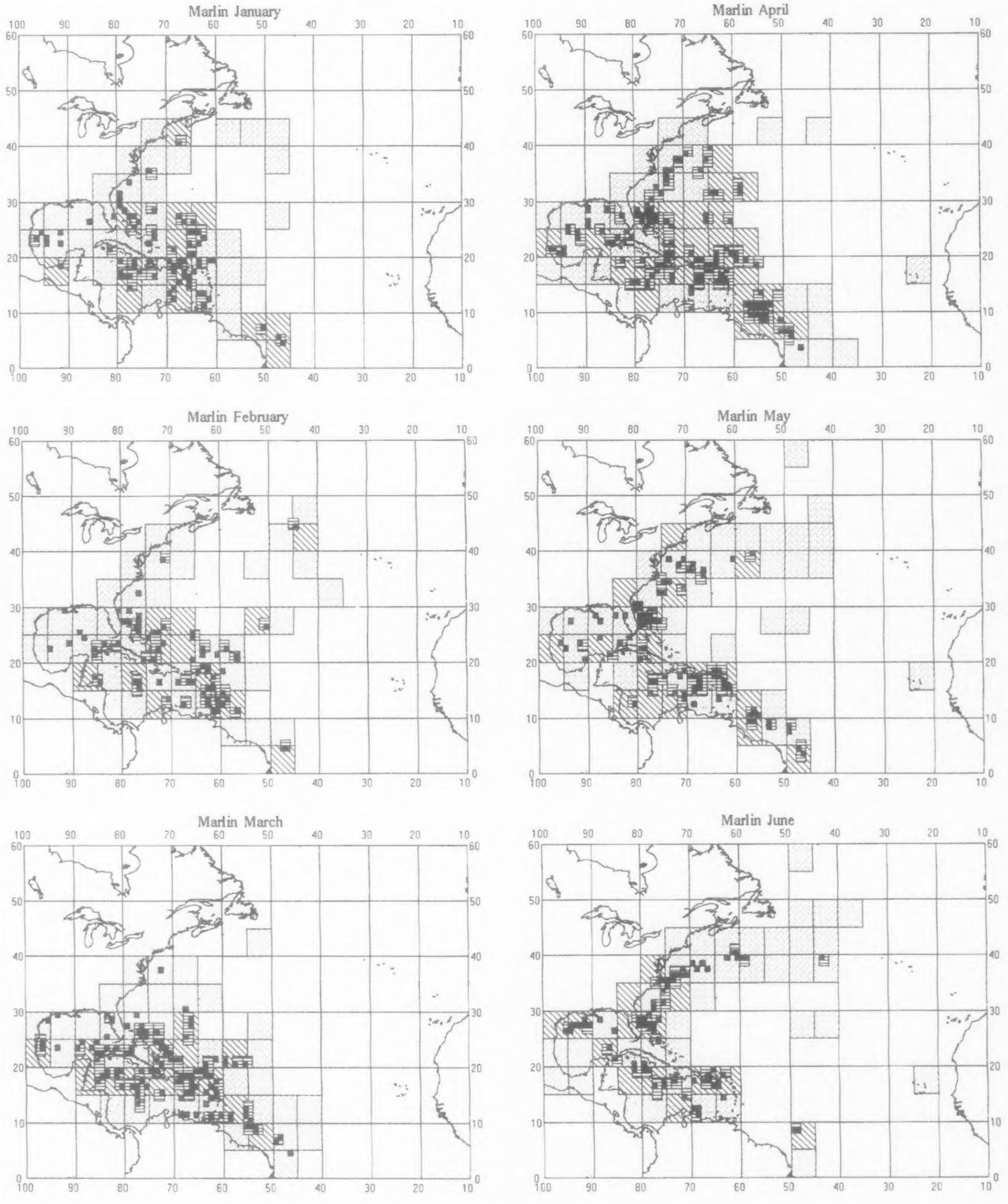
Marlin January
Marlin April
Marlin February
Marlin May
Marlin March
Marlin June
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Figure 4

Distribution of 1986–91 U.S. pelagic-longline fishing effort by month and area fished (stippled or diagonally shaded cells of 5° cell or smaller. Month–area cells where marlin bycatch percentages were greater than the 50% threshold levels for 1° (filled), 2° (horizontal shading), and 5° (diagonal shading) cells. Elimination of the effort in these cells would have reduced the marlin bycatch by 50% and reduced the target species catch by 16.4, 19.6 and 20.7%, respectively.

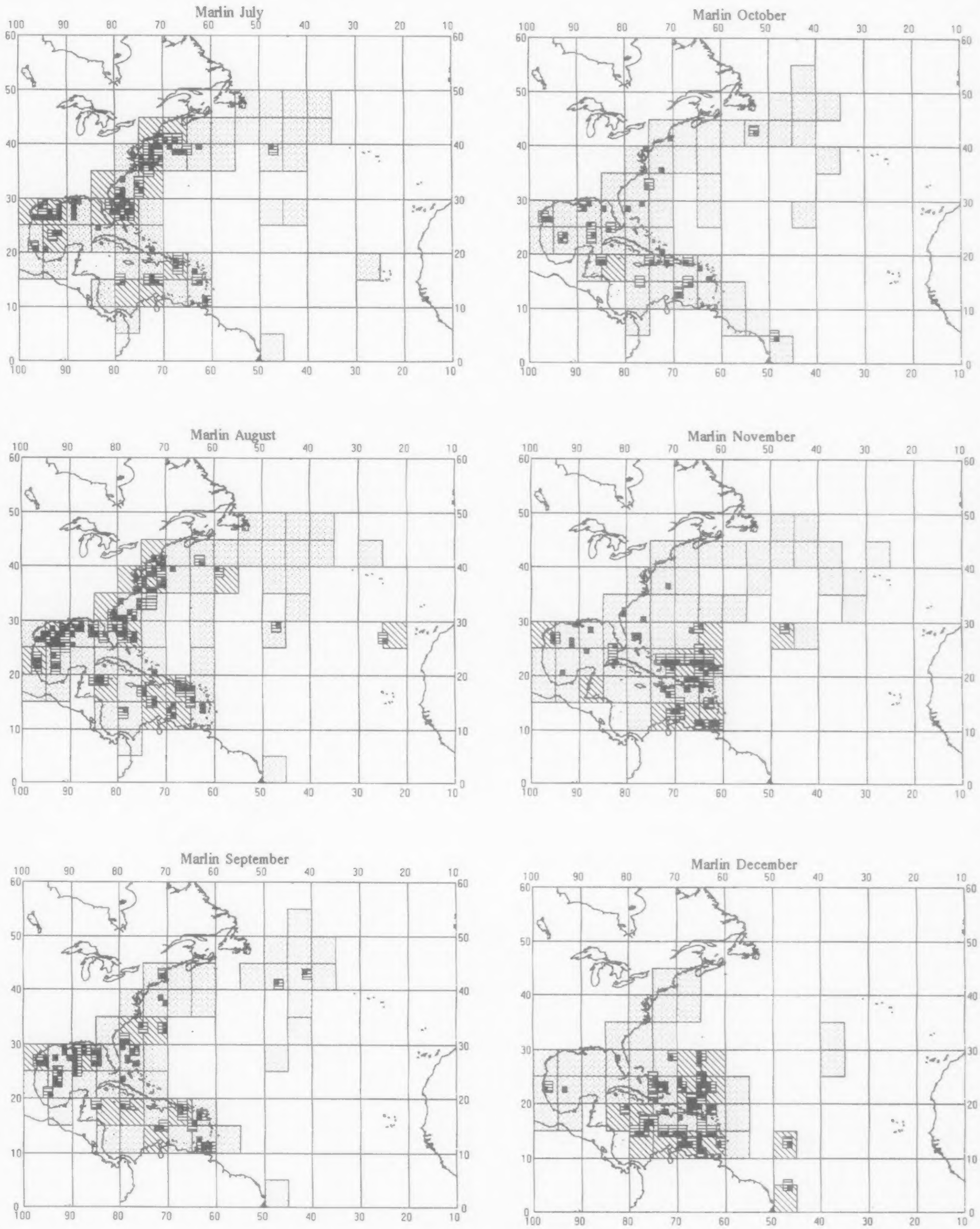
Marlin July
Marlin October
Marlin August
Marlin November
Marlin September
Marlin December
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Figure 4 (continued)

lagic-longline vessels, although the amount of available data for the period is limited.

Although the study results demonstrate that time–area restrictions on the U.S. pelagic-longline fishery could substantially reduce the bycatch of billfish by this fishery, it is only a first step. As Murawski (1992) pointed out, any bycatch reduction plans involving time–area manipulation of the fishery should be economically viable and the proposed program must be effectively implemented and enforced. These issues were beyond the scope of the present study. An evaluation of the utility of time–area restrictions for reducing the mortality of billfish in the longline fishery must also consider aspects of the dynamics of the fishery itself. Among other considerations, the present analysis assumes that the effort eliminated by a time–area closure would not be redirected to some other time or area. The catch associated with a stratum removed by the selection of a particular threshold of percent billfish in the catch was simply removed from the total catch of both the billfish bycatch and target species. With no restriction on total effort, it seems more likely that the affected effort would be redirected into some other area, and the total billfish bycatch, although reduced, would not be reduced by the magnitude indicated in Tables 2 and 3 (and of course, neither would the target species). Analyses that consider the possible redirection of effort would need to include socioeconomic considerations about the nature and dynamics of the pelagic-longline fishery. Also catch limitations arising from the U.S. allocation of total allowable catches of the various target species by ICCAT could be integrated into the analysis. The focus of such an analysis would be to minimize the billfish bycatch by selecting fishing areas that would maximize the catch rates of target species in areas of minimal billfish bycatch. This could both promote efficient use of the target resources and the reduction of billfish bycatch. Similarly, other management objectives could be integrated into the time–area question.

Although, such extensions of the methods presented here should prove fruitful for the selection of actual management restrictions, the results of this study clearly indicate that the relative time and areal distributions of billfish and target species in the pelagic-longline catch are different. This difference can be exploited to reduce the billfish bycatch in this fishery with less than a proportional effect on the catch of targeted species. A next step toward identifying realistic management measures could be the characterization of reasonable, contiguous geographic areas where pelagic-longline closures would be both practical and of the greatest benefit to increased billfish survival. However, because U.S. vessels are a small part of the total Atlantic pelagic-longline fishery, greatest gains from this approach would necessarily involve participation of the pelagic-longline fleets from other countries.

Acknowledgments

This work was supported by The Billfish Foundation. Analyses leading to the results presented in this report were derived by using ICCAT task i and task ii data files, and the U.S. large pelagic logbook data files from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida. I thank analysts of the Sustainable Fisheries Division of the Southeast Fisheries Science Center for their assistance in obtaining and using these databases.

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Abstract.—Sablefish, *Anoplopoma fimbria*, are especially difficult to age. Ages are typically determined by counting growth zones that are assumed to be annuli on the burnt cross section of an otolith. We evaluated the accuracy of ageing methods by comparing the ages obtained from two experienced age readers with those ages that were known. A mark-recapture experiment on sablefish provided a relatively large sample (n=49) of 2–9 year old sablefish. This sample of known-age fish provided a unique opportunity to evaluate the accuracy of ageing methods for young sablefish. Our study generally confirmed the criteria used to age young sablefish. According to the assignment of ages from two experienced age readers, about two-thirds of the fish were misaged. Of these, most fish (81% and 71% for the two readers) were misaged by only one year. After reexamination of the otoliths, most of the discrepancies between reader age and known age could be resolved. Ageing-error matrices that define the probability of assigning an age to a fish of a given true age were estimated from among-reader variability and from comparison of known ages to reader ages. Estimates of ageing errors, based on comparison of known ages to reader ages, were considerably higher than estimates obtained from among-reader variability. We recommend that ageing-error corrections applied in stock assessment models be based on the ageing-error matrix derived from known and reader ages.

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Age validation and analysis of ageing error from marked and recaptured sablefish, *Anoplopoma fimbria*

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Errors in fish ageing may result in biases in stock assessments and possible mismanagement of fisheries. Estimates of natural mortality, age composition, growth parameters, and maturity schedules of a fish population all depend on accurate ageing for their reliability. Thus, valid ageing is a key to understanding the biology and dynamics of fish populations.

Ageing error in stock assessment models can lead to errors in modeling results (Kimura, 1990). Ageing errors tend to smooth differences in year-class strengths and may confound attempts to estimate stock recruitment relationships and to relate year-class strength to environmental factors (Fournier and Archibald, 1982; Richards et al., 1992). Estimation of ageing errors enables such errors to be accounted for by allowing observed ages to be converted back to correct ages (Richards et al., 1992). If misspecified or unaccounted for, ageing error can lead to erroneous yield projections and overfishing (Lai and Gunderson, 1987; Tyler et al., 1989).

Sablefish, aged as old as 63 years in Alaska (Sigler et al., 1997), is an especially difficult species to age (Kimura and Lyons, 1991). Beamish and Chilton (1982) first suggested that sablefish was a much longer-lived species than previously thought and proposed an ageing method using broken and burnt otoliths that would result in more accurate ages. Preliminary data from their tagging studies, otoliths marked with oxytetracycline (OTC), and a small sample (n=6) of known-age fish appeared to validate this new method. Results from subsequent studies with recaptured OTC-marked fish (Beamish et al., 1983; McFarlane and Beamish, 1995), a small sample of pen-reared fish (Lai, 1985), and radiometric ageing (Kastelle et al., 1994) have further substantiated the reliability of this method. This break-and-burn method is now widely accepted by sablefish age readers. Sablefish is still a very difficult species to age, and age determination is highly subject to an age reader's interpretation.

For this paper, sablefish tagged and released as young juveniles (Rutecki and Varosi, 1997a) provided a relatively large sample (n=49) of known-age fish, 2–9 years old when recaptured. This sample provided a unique opportunity to evaluate the accuracy of production ageing methods for young sablefish. "Production ageing" is the routine ageing of large samples of fish, usually to obtain age and growth information or age composition. We conducted a statistical analysis of ageing errors and compared ageing errors based on among-reader agreement with ageing errors based on reader and known-age agreement.

Materials and methods

Known-age fish

From 1985 to 1991 about 23,000 age 0–2 sablefish were tagged with individually numbered Floy anchor tags (Rutecki and Varosi, 1997a, 1997b). By 31 December 1993, 1160 of these fish had been recaptured, mostly from commercial fishing operations; otoliths were taken from 49. In Rutecki and Varosi's studies, cohorts of young (aged 0–2) sablefish were periodically sampled in interior bays of southeastern Alaska from spring through early fall. Depending on the time of year, usually only one or two age classes were present at the sampling locations, and these age classes could be distinguished easily from one another on the basis of nonoverlapping length frequencies (see Figs. 5 and 7 in Rutecki and Varosi [1997b]). Rutecki and Varosi (1997b) confirmed assignment of ages by ageing otoliths from a subsample of the fish measured for length. Of the 49 known-age sablefish, one was tagged at age 0, 41 at age 1, and seven at age 2. Known age of a fish was calculated by subtracting the year of release from the year of recapture and then adding the age at release. For example, the known age of a fish tagged in 1986 at age 1 and recaptured in 1992 would be 7 years.

Ageing methods

Extracted otoliths were stored in a 50% ethyl alcohol solution. A sample of otoliths from 140 fish, including the 49 known-age fish, were aged by two experienced readers in the Age and Growth Laboratory at the Alaska Fisheries Science Center (AFSC) in Seattle, Washington. Using normal production ageing procedures, the readers were told the fork length of each fish and the month and day of sampling. The year of sampling was withheld. Age readers were aware that known-age otoliths were in the sample but did not know what percentage of the sample were known-age specimens nor the age range of the known-age fish.

The primary age reader (hereafter referred to as "primary reader") prepared all the otoliths and was first to examine the sample. The ageing methods generally followed Beamish and Chilton (1982). The ageing routine began with placing each otolith in a water-filled petri dish with a black background and examining it through a light microscope with fiber-optic light. This gave the primary reader a general idea of an age range to expect before the otolith was broken and burned. Next, the otolith was broken dorsoventrally along the focus, and the broken surface was passed over a flame. The burnt half was then mounted into clay for support, and the burnt surface was coated with cedar oil for clarification. The burnt surface consisting of light and dark zones was then examined by using a light microscope and fiber-optic light. The light areas are known as opaque zones and the dark areas as translucent zones. Notes kept by the reader included the reasons for ageing decisions when uncertainties occurred. Typically in production ageing, an age reader may opt not to assign an age to an otolith if the otolith pattern or condition is considered so poor that the reader's confidence at reproducing roughly the same age again is questionable; this policy was followed in our study.

In production ageing at the AFSC, after the primary reader completes the age determinations, another reader (hereafter referred to as the "tester") typically rereads a 20% random sample of the otoliths without knowledge of the primary reader's ages. This is done mainly to control quality (Kimura and Lyons, 1991). Because the known-age specimens were not known to the readers, the randomly chosen 20% sample included only 10 of the known-age otoliths. To compare agreement on all known-age otoliths, a second subsample was drawn, which included all the remaining known-age otoliths interspersed with some unknown-age otoliths. The tester did not know the percent composition of known- to unknown-age otoliths in either subsample.

In addition to the ageing methods of Beamish and Chilton (1982), in production ageing at the AFSC, readers use the marginal increment component for ageing, i.e. they decide whether the most recent year's annulus was formed along the margin of an otolith. Many experienced sablefish age readers have concluded that the annulus usually forms in spring, but some annuli may form in summer. However, an age reader must decide whether an annulus was deposited before the date of otolith collection by considering the date of the otolith collection and the amount of otolith growth between the last annulus and the otolith margin. If the otolith was collected in the spring or summer and there is a relatively large area of growth along the otolith margin, an age reader would probably decide that the annulus had not yet been deposited and would therefore add 1 to the number of annuli observed on the otolith. However, if a relatively small area of growth is seen, then the reader would probably assume that the annulus had been deposited and assign an age equal to the number of annuli observed. By fall and winter, the current year's annulus is expected to have been deposited, and the fish age would, therefore, equal the number of annuli observed on the otolith.

Analysis of ageing errors

Present stock assessment of sablefish and many other groundfish species in Alaska is based on an age-structured model that attempts to estimate the true age composition of the population (Sigler et al.[1]). Ageing errors in catch-age models can be accounted for by supplying an ageing-error matrix (Fournier and Archibald, 1982; Methot, 1990; Richards et al., 1992). This matrix defines the probability of assigning a particular age to a fish with a given true age. The results of multiple age determinations from independent age readings can be used to estimate the ageing-error matrix (Richards et al., 1992). In practice, a normal distribution of observed age for each true age is assumed and because ageing error tends to increase with age, an increase in the standard deviation with increasing age is used (Lai and Gunderson, 1987; Methot, 1990). Use of multiple readings to assess ageing errors cannot detect a systematic difference (i.e. bias) between observed and true ages (Richards et al., 1992).

We constructed two ageing-error matrices to illustrate the possible difference in perceived ageing error based on agreement between primary reader and tester and between reader and known age. The first matrix was based on primary-reader and tester ages and the second was based on reader (both primary reader and tester) and known ages.

Richards et al. (1992) presented a statistical model for estimating ageing error. We used the "normal model" of Richards et al. (1992). For a given true age b, the standard deviation $\sigma(b)$ of the observed age is defined by three parameters σ_1, σ_A, and α such that

$$\sigma(b) = \begin{cases} \sigma_1 + (\sigma_A - \sigma_1)\dfrac{1-e^{-\alpha(b-1)}}{1-e^{-\alpha(A-1)}}; & \alpha \neq 0 \\ \\ \sigma_1 + (\sigma_A - \sigma_1)\dfrac{b-1}{A-1}; & \alpha = 0 \end{cases} . \qquad (1)$$

The σ_1 and σ_A are standard deviations for the minimum and maximum ages, respectively. The parameter α determines the nonlinearity of the function, where $\sigma(b)$ becomes linear in b as α tends to 0. Given the parameter vector $\mathbf{\Phi} = (\sigma_1, \sigma_A, \alpha)$ and observed age classes a, the age-error matrix $q(a \mid b, \mathbf{\Phi})$ is defined by

$$q(a|b,\mathbf{\Phi}) = \frac{x_{ab}(\mathbf{\Phi})}{\sum_{a=1}^{A} x_{ab}(\mathbf{\Phi})}, \qquad (2)$$

where $x_{ab}(\mathbf{\Phi})$ is the discrete normal density function such that

$$x_{ab}(\mathbf{\Phi}) = \frac{e^{-\frac{1}{2}\left[\frac{a-b}{\sigma(b)}\right]^2}}{\sqrt{2\pi}\sigma(b)} . \qquad (3)$$

In Richards et al. (1992), the assumed "true age" for a fish aged by multiple readers is the modal age among multiple readers. We used the mean age rounded to the nearest integer because the mode is not defined for two readings when the ages differ. For the reader and known-age data, the true age is the known age. A value for the maximum age A is required. For the reader and known-age data set, we set A equal to the maximum known age. For the primary reader and tester data set, we set A equal to the maximum assigned age.

The model of Richards et al. (1992) does not include estimation of bias. The use of known ages allows bias to be estimated and incorporated in the ageing-error matrix. By including three additional parameters, Ericksen (1997) generalized the methods of Richards et al. (1992) to include estimation of bias for tag recapture and known-age data. As with Equation 1, for a given true age b, the bias $\beta(b)$ of the observed age is defined by three parameters, β_1, β_A, and λ, such that $\mathbf{\Phi} = (\sigma_1, \sigma_A, \alpha, \beta_1, \beta_A, \lambda)$ and

$$\beta(b) = \begin{cases} \beta_1 + (\beta_A - \beta_1)\dfrac{1-e^{-\lambda(b-1)}}{1-e^{-\lambda(A-1)}}; & \lambda \neq 0 \\ \\ \beta_1 + (\beta_A - \beta_1)\dfrac{b-1}{A-1}; & \lambda = 0 \end{cases} . \qquad (4)$$

Equation 3 is modified to obtain

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[1] Sigler, M. F., J. T. Fujioka, and S. A. Lowe. 1997. Sablefish. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fish. Manage. Council, 605 W 4th Ave., Suite 306, Anchorage, AK 99501.

$$x_{ab}(\mathbf{\Phi}) = \frac{e^{-\frac{1}{2}\left[\frac{a-(b+\beta(b))}{\sigma(b)}\right]^2}}{\sqrt{2\pi\sigma(b)}}. \qquad (5)$$

To estimate the classification matrix defined by Equation 2, maximum likelihood was used to estimate the parameters of the model. The likelihood (L) of the observed ages $\mathbf{A}$ given the true ages $\mathbf{B}$ is

$$L(\mathbf{A}|\mathbf{B}) = \prod_{i=1}^{I}\prod_{j=1}^{J} q(a_{ij}|b_i,\mathbf{\Phi}), \qquad (6)$$

where a_{ij} = the age assigned to fish i by reader j; and
b_i = the true age of fish i.

In practice, the inference function $-2 \log L(\mathbf{A}\,|\,\mathbf{B})$ is minimized to obtain parameter estimates. Given the number of parameters N, the Akaike information criteria (AIC) (Akaike, 1974; Richards et al., 1992),

$$AIC = -2\log L(\mathbf{A}|\mathbf{B}) + 2N, \qquad (7)$$

was used in the model identification process. A model with a low AIC value in relation to other models is considered the best-fit model with the fewest parameters.

Six alternative representations (cases) of ageing error were considered in the analysis. The different cases represented the two different data sets, full models, and models reduced by parameter constraints (Table 1). Although not within the scope of our study, we recognize other alternative model specifications may be appropriate for these data sets. For example, a classification matrix with skewed distributions of the probability of assigning an age to a fish of a given true age may be appropriate.

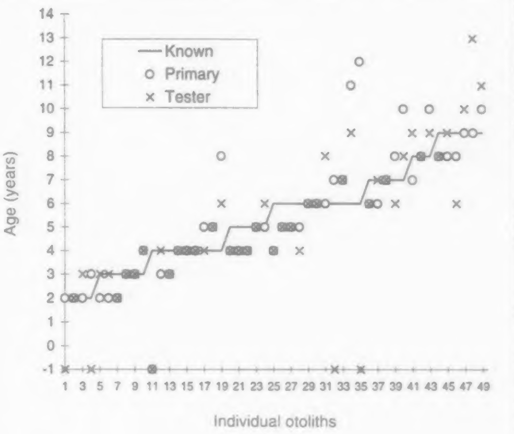

Figure 1

Comparison of known age with ages obtained by two age readers for 49 sablefish. A value of −1 for a age denotes the reader chose not to age the given sample. The x-axis has been sorted by known age from youngest to oldest.

Table 1

Alternative cases for analysis of ageing error based on primary reader and tester data (data set 1) and reader and known-age data (data set 2).

Case	Data set	Parameters	Constraints
1	1	$\sigma_1, \sigma_A, \alpha$	—
2	1	σ_1, σ_A	$\alpha = 0$
3	2	$\sigma_1, \sigma_A, \alpha, \beta_1, \beta_A, \lambda$	—
4	2	$\sigma_1, \sigma_A, \alpha, \beta_1, \beta_A$	$\lambda = 0$
5	2	$\sigma_1, \sigma_A, \beta_1, \beta_A, \lambda$	$\alpha = 0$
6	2	$\sigma_1, \sigma_A, \beta_1, \beta_A$	$\lambda = 0; \alpha = 0$

Results and discussion

Comparison of reader ages to known ages

The primary reader ages agreed with the known ages in 35.4% of the cases (Fig. 1). Of the 49 known-age sablefish otoliths, the primary reader chose not to age one specimen because of the poor condition of its otoliths. Of the 31 misaged fish, the primary reader misaged most (80.6%) by 1 year: 17 of the 18 underaged fish and 8 of the 13 overaged fish. In three cases (known ages=4, 6, and 6 years), the primary-reader ages differed substantially at 8, 11, and 12 years.

Results for the tester were generally similar to those of the primary reader. The tester age agreed with the known age in 38.6% of the 44 total otoliths that the tester aged (Fig. 1), and 5 otoliths were considered unreadable. Of the testers's misaged fish, most (70.1%) were misaged by 1 year: 10 of the 13 underaged fish and 9 of the 14 overaged fish. The largest discrepancy was 4 years: known age was 9 years and tester age was 13 years.

Agreement between primary reader and tester ages was much greater than between the known and primary-reader ages or the known and tester ages (Fig. 1). Primary reader and tester matched ages in 24 of the 44 (54.5%) specimens compared, indicating that they interpreted annuli similarly. Most discrepancies (n=12; 60.0%) were discrepancies of one year. The primary reader tended to age the fish younger than the tester: 12 less than tester ages and 8 greater. Only once did their ages differ by more than two years (known age=9; primary reader=9; tester=13).

Table 2

Comparison of parameter estimates for alternative models of ageing error for sablefish based on primary reader and tester data (data set 1) and reader and known-age data (data set 2). Number of observations (*n*), maximum age (*A*), number of parameters (*N*), minimum values of the inference function (*l*), and Akaike information criterion (*AIC*) are also given.

Case	Data set	n	A	N	σ_1	σ_A	α	β_1	β_A	λ	l	AIC
1	1	88	13	3	0.399	2.464	–0.358	—	—	—	139.3	145.3
2	1	88	13	2	0.270	1.094	set to 0	—	—	—	143.1	147.1
3	2	92	9	6	0.253	1.792	0.341	–0.284	0.289	0.116	308.8	320.8
4	2	92	9	5	0.213	1.796	0.346	–0.191	0.307	set to 0	308.9	318.9
5	2	92	9	5	0.911	1.948	set to 0	–1.731	0.276	0.604	310.0	320.0
6	2	92	9	4	0.699	2.089	set to 0	–0.340	0.433	set to 0	310.4	318.4

This study generally confirmed the criteria used for ageing young sablefish. Even though a high proportion of fish were misaged, most fish were misaged by only one year. In addition, after reexamining the otoliths after the known ages had been revealed, the primary reader could reconcile the differences between the known and assigned ages in most cases (25 of 31). Anderl and Heifetz[2] have described three types of misinterpretation of otolith patterns that resulted in most misages: 1) misinterpretation of an ambiguous check (i.e. false annulus) immediately following the first annulus; 2) misinterpretation in assessing whether the most recent year's annulus had been formed; and 3) misinterpretation of multiple checks on parts of the otolith (a check is a mark, growth zone, or part of a growth zone on an otolith that does not form annually but reflects various environmental or physiological changes [Chilton and Beamish, 1982]).

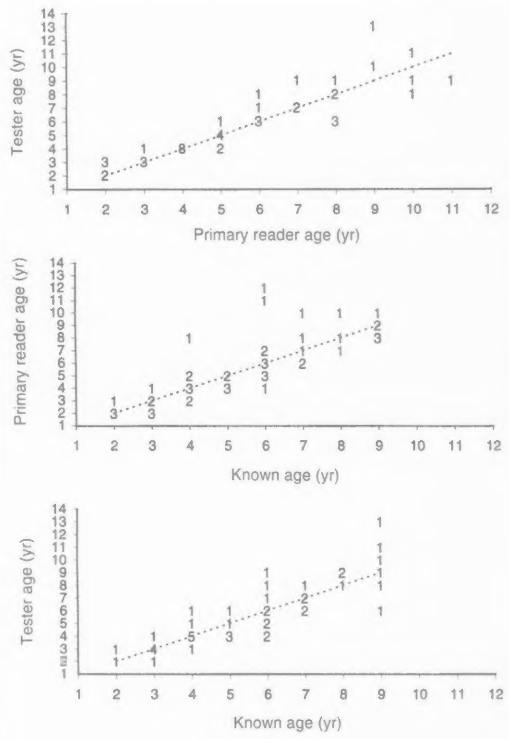

Figure 2

Observed relation for sablefish between primary reader age and tester age, known age and primary reader age, and known age and tester age. Points are represented by the frequency distribution of observations. A dotted line of slope 1 is included for reference in each panel.

Analysis of ageing errors

Table 2 summarizes the parameter estimates for various model specifications from the data in Figure 2. The estimates based on between-reader variability include only data where both primary reader and tester readings were available. The data consisted of $I = 44$ fish and $J = 2$ readings per fish resulting in $n = 88$ observations. The estimates based on reader and known ages were derived from data where at least one reader determined an age. The data consisted of $I = 44$ fish with $J = 2$ readings per fish and $I = 4$ fish with $J = 1$ reading per fish resulting in $n = 92$ observations.

For the estimates that included only between-reader variability, a model with all three parameters estimated (case 1) provided the best fit with the fewest parameters (i.e. lowest AIC values). The AIC value for a model with α constrained to 0 (case 2) was nearly

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[2] Anderl, D., and J. Heifetz. 1999. An evaluation of ageing criteria for sablefish based on known age specimens. In prep.

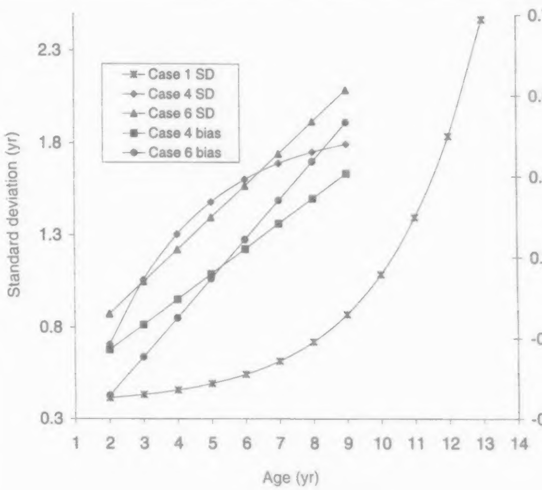

Figure 3

Estimated standard deviation (SD) and bias of observed age of sablefish for each true age based on primary-reader and tester ages (case 1) and reader and known ages (case 4 and case 6). Case refers to model specifications listed in Table 1.

2 units above the AIC value for case 1. For the reader and known-age data set, a model with α and λ constrained to 0 (case 6) provided the best fit with the fewest parameters. The AIC value for a model with only λ constrained to 0 (case 4) was only 0.5 units above the minimum. The closeness of the AIC values for these two cases indicates that case 6 provides only a slightly better model fit than case 4. The difference between case 4 and case 6 is best understood by comparing estimated standard deviation and bias at age (Fig. 3). Case 4 results in a nonlinear relationship between standard deviation and age, and the standard deviation approaches an asymptote near age 9; whereas for case 6, the standard deviation increases linearly with age. Bias is linear for both cases, and case 6 has higher absolute bias than case 4 for most ages.

Estimates of ageing errors based on comparison of known ages to reader ages were considerably higher than estimates obtained from between-reader variability (Fig. 4). For example, for age 2–9 fish, according to primary reader and tester ages, the estimates of the probability of assigning the true age was 0.95–0.46. In contrast, according to the estimates from reader and known ages, the probability was only 0.71–0.19. This discrepancy was expected because agreement between readers was considerably greater than between reader and known ages. Thus, use of between-reader agreement to assess ageing error may lead to a false sense of the true error.

In conclusion, use of ageing errors based on known-age samples may help improve stock assessment of sablefish. Future analysis of ageing errors for sablefish may require consideration of the time of year otoliths are taken because, as Anderl and Heifetz[2] have shown, ageing error may depend on the season when an age sample is taken. Precaution should be taken in extending our results to fish older than age 9. Results should be compared between stock assessments that use parameter estimates for the ageing-error matrix based on case 4 and case 6. If a sample is obtained that includes older known-age fish, the ageing-error matrix can be estimated for older fish. We expect such a sample to be available in the future as the fish tagged as juveniles by Rutecki and Varosi (1997a) continue to be recovered. For many species other than sablefish, known-age specimens are not available. For such species, variability between readers may be the only data available to assess ageing error. Such data are valuable for evaluating the precision and consistency of ageing criteria applied by different readers. Estimates derived solely from between-reader variability should be viewed as minimum estimates of ageing error.

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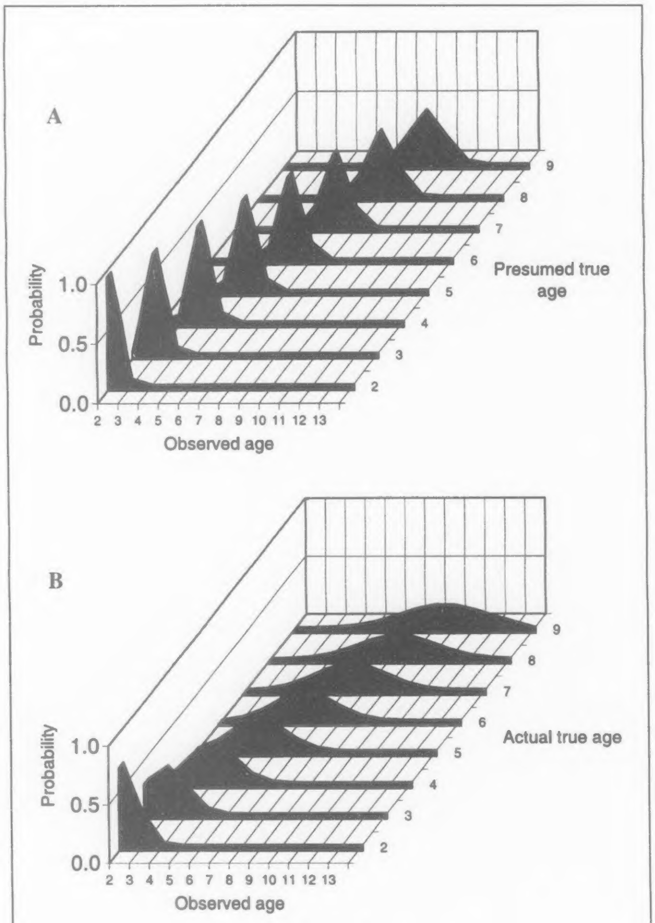

Figure 4

Estimated probability of observing a given age for a particular true age of sablefish estimated from primary-reader and tester ages (**A**, case 1) and from reader and known ages (**B**, case 6). Case refers to model specifications listed in Table 1.

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Distribution and abundance of shortraker rockfish, *Sebastes borealis*, and rougheye rockfish, *S. aleutianus*, determined from a manned submersible

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Abstract.–A manned submersible was used in the eastern Gulf of Alaska in 1992 to observe spatial distributions and habitats of shortraker rockfish, *Sebastes borealis*, and rougheye rockfish, *S. aleutianus*, on the continental slope at 262–365 m depths. Observations of these two species were combined because distinguishing between them was not always possible from the submersible. A seafloor area of 104,900 m^2 was surveyed at 15 dive sites, and 646 shortraker and rougheye rockfish were observed. Densities were 0.0 to 14.8 rockfish/1000 m^2 (mean, 5.8 rockfish/1000 m^2). Of the 646 rockfish, 115 were observed above bottom and 531 were on the bottom. The above-bottom rockfish were descending slowly to the seafloor and became sedentary when they contacted the seafloor. Approximately two-thirds of the rockfish were in groups; 82 of the 113 groups contained 2 or 3 rockfish, and only 2 groups had more than 12 rockfish. Rockfish were associated with 20 of the 22 substrates encountered. Soft substrates of sand or mud usually had the greatest densities of rockfish, whereas hard substrates of bedrock, cobble, or pebble usually had the least densities. Habitats containing steep slopes and numerous boulders had greater densities of rockfish than habitats with gradual slopes and few boulders; 52 rockfish lay against boulders. According to catch rates from bottom-trawl surveys, populations of shortraker and rougheye rockfish may be underestimated because of the above-bottom distribution of these rockfish and their use of steep-slope boulder habitats.

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Fishery Bulletin 97:264–272 (1999).

Shortraker rockfish, *Sebastes borealis*, and rougheye rockfish, *S. aleutianus*, occur in commercial quantities from northern Washington throughout Alaska (Allen and Smith, 1988). Both species are similar in appearance and share similar life-history patterns. These rockfish attain maximum total lengths of about 100 cm (Kramer and O'Connell, 1986) and have been aged at more than 120 years (Chilton and Beamish, 1982). Their bathymetric range is 25–875 m (Allen and Smith, 1988), and their lengths at 50% maturity are 43.97 cm for rougheye rockfish and 44.90 cm for shortraker rockfish (McDermott, 1994). They apparently share similar habitats. During the 1996 Gulf of Alaska triennial survey, 89% of the trawl hauls containing shortraker rockfish also contained rougheye rockfish.

Shortraker and rougheye rockfish are harvested with bottom trawls and longlines in the Gulf of Alaska. Until the mid 1980s, they were mainly bycatch species caught during longlining for halibut, *Hippoglossus stenolepis*, and sablefish, *Anoplopoma fimbria*, and during bottom trawling for more abundant rockfish species. Before 1991, shortraker and rougheye rockfish were combined with 18 other rockfish species and managed as "slope rockfish." Since 1991, shortraker and rougheye rockfish have been managed as a separate subgroup because fishermen target these highly valued species. For example, shortraker and rougheye rockfish made up 33% of the commercial rockfish catch in the eastern Gulf of Alaska in 1990 but made up only 14% of the estimated rockfish biomass (Heifetz and Clausen, 1991). Catch quotas of shortraker and rougheye rockfish are based primarily on population estimates derived from catch rates of bottom-trawl surveys (Heifetz et al., 1996). These estimates are suspect because the catch efficiency of bottom trawls on these species is unknown and only certain types of habitats can be sampled with bottom trawls.

Catch rates from bottom-trawl surveys are converted to biomass estimates by assuming a 100% sampling efficiency for the area swept by the trawl. The area that is swept is determined as the distance between the wingtips of the net and the distance the net is towed. The sampling efficiency could be less than 100% if fish are distributed above the headrope, protected by structures such as boulders, swim out of the path of the net, or escape under the net. Conversely, if fish are herded into the trawl by the bridles and doors and do not escape above or under the net, the sampling efficiency may be greater than 100%. Typically, smooth (trawlable) substrates are sampled during trawl surveys. Catch rates from trawlable substrates are then applied to all substrates for estimating biomass. Bottom-trawl surveys may not provide reliable biomass estimates of shortraker and rougheye rockfish because 1) the sampling efficiency may not be 100% for the distance between the wingtips of the net, 2) these species may use untrawlable substrates at a different rate than they do trawlable substrates, and 3) the sampling frequency may not be sufficient, depending on the distribution patterns of the target species.

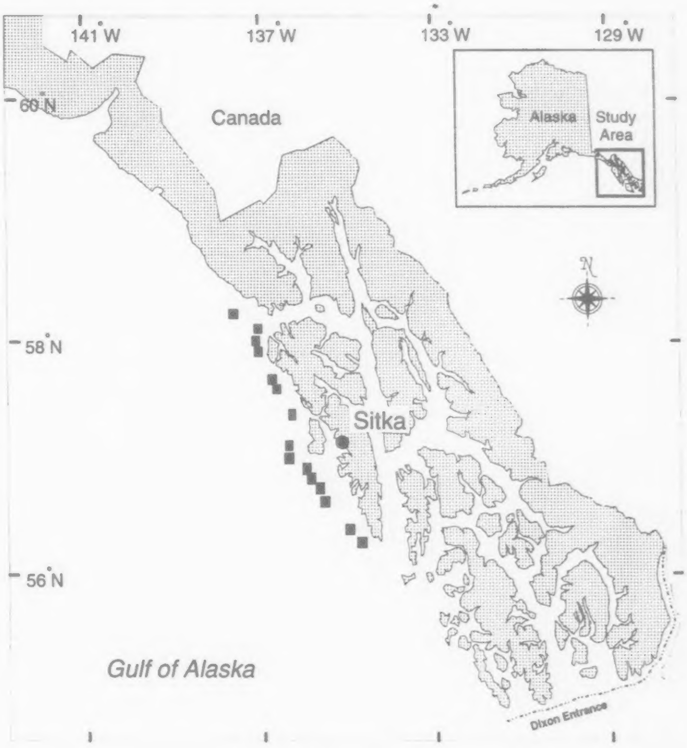

Figure 1

Submersible survey sites for shortraker and rougheye rockfish in the eastern Gulf of Alaska in May 1992.

Minimal information is available on the distribution of shortraker and rougheye rockfish. Fishermen report that rockfish school above bottom in steep-slope areas. From a manned submersible Krieger (1992) observed 20 shortraker rockfish on the continental shelf; these fish were in contact with the seafloor and were distributed as solitary individuals on shallow-sloped, smooth habitat. Shortraker rockfish were observed only at sites where boulders were common, and six of the fish were found next to boulders 0.5–1.5 m in diameter (Krieger, 1992). Catches of shortraker and rougheye rockfish during longline surveys indicate they are most abundant on the upper continental slope at 300–400 m depths (Sigler and Zenger, 1994), but most of this substrate is considered untrawlable and is seldom sampled during bottom-trawl surveys. For example, only eight trawl hauls were completed along the 500-km continental slope in southeastern Alaska during the last four bottom-trawl surveys (1987, 1990, 1993, 1996).

We need to understand the distribution and habitats of shortraker and rougheye rockfish to assess them effectively with bottom trawls or other sampling gear. In this study, a manned submersible was used to observe their spatial distributions and habitat associations. These species were also quantified from the submersible for comparison with abundance estimates from bottom-trawl surveys. The two species were combined and are referred to as rockfish in this paper because distinguishing between them was not always possible from the submersible.

Materials and methods

Study area

This study was conducted in May 1992 on the upper continental slope in the eastern Gulf of Alaska between lat. 56°10' and 58°10'N (Fig. 1). This region has consistently produced high catch rates of shortraker and rougheye rockfish during the annual longline surveys in the Gulf of Alaska (Rutecki et al., 1997). The study area spanned more than 200 km to include a variety of habitats. Distances separating adjacent sites ranged from 0.2 to 84.2 km. Dives were conducted during daylight, between 0600 and 1900 hours.

Submersible

The two-man submersible *Delta* was chartered for all dives. This battery-powered submersible is 4.7 m long, dives to 365 m, and travels 2–6 km/h for 2–4 h. It is equipped with halogen lights, internal and external video cameras, magnetic compass, directional gyro compass, underwater telephone, and transponder that allow tracking of the submersible from a surface vessel. On each dive, the submersible descended to 265–365 m and then usually traveled parallel to the shelf break, followed by up-slope travel to less than 300 m before it ascended. The surface vessel recorded LORAN fixes at the beginning and end of a dive, and every 1–5 min during a dive. The submersible traveled 1.0–2.5 km/h, depending on the slope and ruggedness of the terrain and the magnitude and direction of the current. The degree of slope determined how observations were made from the submersible. When the slope was less than 60°, the submersible remained in contact with the seafloor while the scientist viewed the water column parallel to the seafloor through a starboard porthole 0.5 m above the base of the submersible. When the slope was greater than 60°, the submersible traveled 2–3 m away from the seafloor while the scientist viewed the water column almost perpendicular to the seafloor through portholes on the starboard side and bow. The pilot sat above the observer in a tower with a panoramic view and assisted in locating fish, especially above the submersible. The submersible lights provided constant illumination.

Data analysis

Observations of rockfish and their habitat were audiotape- and videotape-recorded for subsequent analysis and verification. The senior author reviewed all video tapes by 1-min segments (16–42 m travel distances), and four habitat parameters were estimated: 1) main substrate, 2) secondary substrate, 3) slope, and 4) boulder abundance. The main substrate made up 50–100% of the substrate, whereas the secondary substrate made up 10–50% of the substrate. Substrates consisted of mud, sand, pebble, cobble, and bedrock. Granular size used to separate pebble and cobble was 2.5 inches (64 mm), and to separate cobble and boulders was 10 inches (256 mm). Mud would stay suspended when disturbed by the submersible, whereas sand would not. Size references for classifying pebble, cobble, and boulders included the known length and width of a video frame as well as the known, uniform size of invertebrates such as sea stars and shrimp. The slope was classified into four categories: 1 = 0–5°, 2 = 6–20°, 3 = 21–45°, and 4 = 46–90°. Slope classification was based on estimates by the pilot and on the view from a downward-aimed, mounted video camera. Boulder abundance was classified into five categories: 0 = absent, 1 = scarce, 2 = scattered patches, 3 = common (usually in view), and 4 = abundant (always in view). For each site, we calculated the average slope, average boulder abundance, and the densities of rockfish associated with each substrate. For all sites combined, we calculated rockfish densities associated with each substrate, and the percentage of rockfish associated with each slope category and each boulder category.

Rockfish observations included number, size, grouping behavior, above-bottom distribution, and movements. Three sizes of rockfish were estimated visually: small (<30 cm), medium (30–60 cm), and large (>60 cm). The observers had used laser beams to measure rockfish lengths from submersibles and were, therefore, experienced in sizing them. Rockfish were considered grouped if they were within 5 m of each other. Densities were estimated from counts of rockfish and the total seafloor area surveyed. The surveyed area was the distance the submersible traveled (0.3–1.8 km/dive) multiplied by the estimated viewing distance from the submersible (4–10 m, depending on water clarity). These estimates were calibrated against sonar readouts when the seafloor became visible during descents and when the seafloor disappeared from view during ascents. Estimated distances were within 1 m of true distances according to sonar readouts and distance calibrations in previous studies (Krieger, 1993). Rockfish movement rates were based on the estimated distance moved during a specific time period.

Results

Submersible dives

Fifteen submersible dives were completed and 104,900 m^2 of seafloor was surveyed at 262–365 m depths (Table 1). Rockfish densities ranged from 1.2 to 14.8 rockfish/1000 m^2 (mean, 5.8/1000 m^2) at the 14 sites where they were observed. Of the 646 rockfish observed, 188 were small, 289 medium, and 169 large.

Above-bottom and on-the-bottom behavior

We observed 115 rockfish 1–10 m above bottom and 531 on the bottom (Table 2). Sites 5 (80 above-bottom rockfish) and 13 (19 above-bottom rockfish) accounted for 86% of the above-bottom rockfish. Above-bottom rockfish were medium-size (108 rockfish) or large (7 rockfish), and they were observed descending at less than 10 m/min without detectable movements of fins or body. They would contact the seafloor without disturbing sediments and would orient broadside to the current, which would tilt them 10–45° (Fig. 2). Currents were less than 1.0 km/h at all sites.

Table 1

Number and density of shortraker and rougheye rockfish at 15 submersible dive sites in the eastern Gulf of Alaska, 1992. Small = <30 cm; Medium = 30–60 cm; Large = >60 cm.

Site	Depth (m)	Surveyed area (1000 m^2)	Number of rockfish				Density of rockfish (no./1000 m^2)
			Total	Small	Medium	Large	
1	365–262	8.1	25	16	7	2	3.1
2	323–270	1.8	0	0	0	0	0.0
3	346–285	3.5	21	10	6	5	6.0
4	362–262	10.1	60	30	26	4	5.9
5	365–292	13.0	192	24	165	3	14.8
6	365–270	7.9	43	16	19	8	5.4
7	365–270	4.0	5	3	0	2	1.2
8	365–275	7.5	45	7	9	29	6.0
9	365–300	13.5	16	0	3	13	1.2
10	365–270	1.7	21	10	6	5	12.4
11	365–304	7.3	64	28	15	21	8.8
12	365–280	2.0	17	3	3	11	8.5
13	365–320	16.3	98	29	23	46	6.0
14	365–288	5.8	34	9	5	20	5.9
15	365–285	2.4	5	3	2	0	2.1
Totals		104.9	646	188	289	169	

Table 2

The number of shortraker and rougheye rockfish observed on the bottom, above bottom, solitary, and grouped, and their distribution by group size at 15 submersible dive sites in the eastern Gulf of Alaska, 1992.

Site	Fish on bottom	Fish above bottom	Solitary fish	No. of fish in groups	No. of groups	Group size													
						2	3	4	5	6	7	8	9	10	11	12	—	15	32
1	24	1	15	10	4	2	2												
2	0	0	0	0	0														
3	21	0	14	7	2	1			1										
4	59	1	30	30	11	6	3	1	1										
5	112	80	35	157	27	9	6	2	3	1				1	1	2		1	1
6	42	1	19	24	9	6	2			1									
7	5	0	5	0	0														
8	39	6	10	35	10	4	4			1			1						
9	15	1	9	7	3	2	1												
10	21	0	6	15	6	3	3												
11	62	2	37	27	11	8	1	2											
12	17	0	7	10	3	1		2											
13	79	19	21	77	22	13	1	3	1	1		2	1						
14	30	4	22	12	5	4		1											
15	5	0	5	0	0														
Totals	531	115	235	411	113	59	23	11	6	4	0	2	2	1	1	2		1	1

Of the 531 rockfish on the bottom, only 21 moved when passed or approached by the submersible; 5 moved 0.5–1.0 m above the seafloor and swam less than 5 m away at a speed of less than 1 km/h, and 16 moved less than 2 m along the seafloor by drifting or by slight movements of fins. The submersible drifted against several large rockfish, which did not respond as they were pushed along the seafloor.

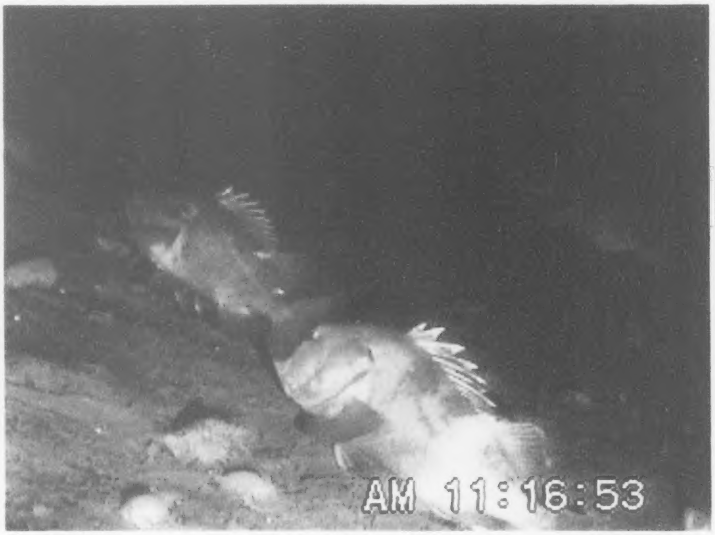

Figure 2

Shortraker or rougheye rockfish tilted with the current while lying on the seafloor in the eastern Gulf of Alaska in May 1992. Observed from a submersible.

Spatial distribution

Of the 115 above-bottom rockfish, 106 were grouped with at least one other rockfish as they descended together to the seafloor. They contacted the seafloor within 5 m of at least one other rockfish in the group. Because these fish maintained a <5-m spacing from each other, all rockfish within 5 m of other rockfish on the seafloor were considered grouped. Twelve sites had 411 grouped fish, and 14 sites had 235 solitary fish (Table 2). Most groups were small; 82 of the 113 groups contained only 2 or 3 rockfish, whereas only two groups contained more than 12 rockfish. Twenty-six pairs of rockfish consisted of a small and medium-size fish separated by less than 0.5 m.

Substrate associations

Twenty-two combinations of primary and secondary substrates were encountered at the 15 sites (Table 3). Substrates changed frequently within each site, averaging 6.9 substrates/site. Rockfish were associated with 20 of the substrates, but no consistent pattern of association was observed within a site. For example, the 8 greatest densities (>16 rockfish/1000 m^2) included 7 different substrates, the 23 lowest densities (no rockfish) included 13 different substrates, and 3 substrates had both more than 16 rockfish/1000 m^2 and no rockfish.

For all sites combined, the most abundant substrate was cobble with sand (17.3%), whereas 7 of the 22 substrates made up 1.0% or less each of the total substrate (Table 4). The greatest densities of rockfish were usually associated with soft substrates. Sand with mud had the greatest average density (9.1 rockfish/1000 m^2), and 7 of the 10 greatest densities were associated with primary substrates of sand or mud. Nine of the 12 lowest densities of rockfish were associated with primary substrates of cobble, rock, or pebble.

Boulder and slope associations

Average boulder indices ranged from 0.0 to 2.1 (Table 3) and were not highly correlated (r=0.30) with rockfish densities. For all sites combined, high-abundance boulder habitat contained greater densities of rockfish than did low-abundance boulder habitat (Fig. 3). Habitats where boulders were absent (index=1) or rare (index=2) were encountered 67% of the time and had 56% of the rockfish, whereas habitats where boulders were more abundant (index=3, 4, or 5) were encountered 33% of the time and had 44% of the rockfish; 52 rockfish were found lying against boulders (Fig. 4). The only site without boulders (site 2) was the only site not containing rockfish.

Average slope indices ranged from 0.9 to 3.7 and were not highly correlated (r=0.56) with rockfish

Table 3

Densities of shortraker and rougheye rockfish associated with specific substrates at 15 submersible dive sites in southeastern Alaska, 1992, and indexes of boulder abundance and topography (slope). Indexes are averages of 1-min video segments, where boulders were absent (0), rare (1), scattered patches (2), common (3), or abundant (4), and slopes were 0–5° (1), 5–20° (2), 20–45° (3), or 45–90° (4). M = mud; S = sand; C = cobble; P = pebble; R = rock; M-S = mud and sand; M-C = mud and cobble, etc.

			Rockfish densities (no./1000 m^2) and associated substrates																					
Site	Boulder index	Slope index	M	M-S	M-C	M-P	M-R	S	S-M	S-C	S-P	S-R	P-S	P-M	P-C	C	C-S	C-M	C-P	C-R	R	R-S	R-M	R/P
1	1.1	2.0						3.1		3.1	2.1		4.1		3.1	3.1	2.1		2.2					
2	0.0	2.0								0.0			0.0		0.0		0.0		0.0					
3	0.7	3.0			4.0	12.8				12.0	8.0				0.0		1.0		0.0					
4	1.1	3.0	0.0	11.8		12.8	0.8		3.0	5.9	8.9		7.9	9.6			4.9							
5	1.7	2.9		5.1				22.3	70.9	9.7							16.9							
6	1.2	3.5	0.0		8.7	4.0				1.9			13.0		5.8		5.8	0.0	0.0			17.3	6.7	2.9
7	1.6	2.0									0.8		3.2	1.1					0.8					
8	2.1	2.0	3.0			0.0		6.5	6.0	6.0	7.4						0.0							
9	0.8	0.9	1.0		1.3	3.9							1.6	0.0	0.5		1.1	0.0	0.0	0.0				
10	0.4	3.7		13.7						25.1							0.0							
11	0.7	3.7		6.5	25.8	12.9				0.0	6.5		9.0		3.2		17.7		6.5					
12	1.1	3.0															11.7		7.6					
13	1.7	3.2						14.0		3.0	5.4		6.0		5.5		9.5		7.5		3.0	3.0		3.0
14	1.9	2.9								11.7	28.0	1.7				0.0	4.9					5.9		
15	1.2	2.4						0.0		4.5		0.0					4.5			0.0		4.5		

densities (Table 3). For all sites combined, habitats with slopes greater than 20° contained greater densities of rockfish than those with slopes less than 20° (Fig. 5). Slopes less than 20° were encountered 37% of the time and had 24% of the rockfish, whereas slopes greater than 20° were encountered 63% of the time and had 76% of the rockfish.

Submersible counts versus trawl catch rates

During the last four bottom-trawl surveys (1987, 1990, 1993, 1996), eight trawl hauls were completed on the continental slope in southeastern Alaska and 234,100 m^2 of seafloor was sampled. The mean catch rate was 3.2 rockfish/1000 m^2 for the 8 trawl hauls, compared with the mean observation rate of 5.8 rockfish/1000 m^2 at the 15 dive sites. Catch rates exceeded 5.0 rockfish/1000 m^2 at only 2 of the 8 trawl sites, whereas observation rates exceeded 5.0 rockfish/1000 m^2 at 10 of the 15 dive sites.

Discussion

Because the two rockfish species were combined in this study, we did not determine whether shortraker rockfish behavior differs from rougheye rockfish behavior. They appear to share the same habitats, based on bottom-trawl sampling and observations from the submersible, but differences may exist in

Table 4

The percentage of each seafloor substrate and density of shortraker and rougheye rockfish associated with each substrate observed during 15 submersible dives in southeastern Alaska, 1992.

Substrate type	Substrate (%)	Rockfish (no./1000 m^2)
sand-mud	1.0	19.1
cobble-sand	17.3	9.7
mud-cobble	1.7	9.3
sand	6.5	8.4
mud-pebble	5.0	7.0
sand-cobble	10.0	6.7
rock-mud	2.0	6.7
mud-sand	7.5	6.1
rock-sand	3.6	6.0
sand-pebble	10.5	5.5
pebble-mud	2.4	5.5
pebble-sand	11.5	3.7
cobble-pebble	7.7	3.5
rock	0.6	3.0
rock-pebble	1.0	3.0
pebble-cobble	6.0	2.5
cobble-rock	0.5	2.1
sand-rock	0.6	1.5
mud	2.1	0.9
mud-rock	1.1	0.8
cobble-mud	0.8	0.0
cobble	0.4	0.0

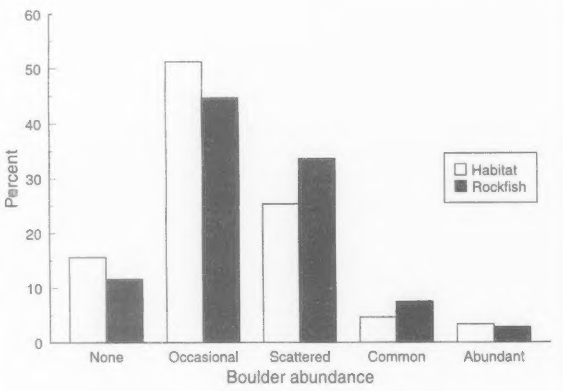

Figure 3

Five levels of boulder abundance observed on the seafloor, and the percent occurrence of habitat and percent occurrence of shortraker and rougheye rockfish associated with each level. Observations are from a submersible in the eastern Gulf of Alaska, 1992.

their above-bottom distributions, grouping behavior, and use of boulders.

The 150 rockfish observed above bottom were at nine different dive sites and all were descending, indicating they were reacting to the submersible. They were probably seeking the seafloor in response to the submersible. A diving response to trawl and vessel disturbances has been noted for other species of offshore rockfish (Kieser et al., 1992). The protection provided by the seafloor may explain their reluctance to move when they are on the seafloor and approached by the submersible. Assuming rockfish were descending in response to the submersible, the proportion of rockfish observed above bottom is probably a minimum estimate because some had probably reached the seafloor before they were viewed from the submersible. The 80 rockfish above bottom at site 5 indicate that a high percentage of rockfish move above the seafloor, although the frequency and duration of their movements are unknown. Rockfish may move above bottom to capture prey such as the squid and lantern fish (Myctophidae) on which they are known to feed (Yang, 1993, 1996). About two-thirds of the rockfish were in groups of 2–6 fish; only two groups contained more than 12 fish. The reason for the close pairing of a small and medium rockfish is unknown; it is probably not related to mating because female shortraker and rougheye rockfish shorter than 30 cm are not mature (McDermott, 1994).

The spatial distribution of rockfish varied within dive sites. This variability can be partially explained by their grouping behavior and by their habitat associations. Rockfish were associated with most of the habitats encountered, but the greatest densities were associated with soft substrates, frequent boulders, and slopes greater than 20°. Their association with soft substrates may be prey related. Pandalid shrimp and hippolytid shrimp, which concentrate on soft substrates, were the main prey of rougheye rockfish examined from the Gulf of Alaska (Yang, 1993, 1996) and from the Aleutian Islands (Yang, 1996). The association of rockfish with boulders in this study and on the continental shelf (Krieger, 1992) indicates that boulders are important for these species. Perhaps boulders are a necessary habitat feature, because shortraker and rougheye rockfish were absent at the one site without boulders in this study and at the three sites without boulders in a previous study (Krieger, 1992). These species may use boulders as territorial markers, to avoid currents, or to capture prey. Rockfish were least abundant on shallow-slope habitat (<5°) in this study, and Krieger (1992) observed shortraker rockfish at three sites where the slope was 3–12° but none at six sites with slopes less than 2°. Steep slopes may provide relief from currents.

The mean observation rate from the submersible was about twice the mean catch rate from bottom-trawl surveys, probably because of the limited habitats sampled during trawl surveys. Bottom trawling may be effective for sampling shortraker and rougheye rockfish on low-relief habitats because these rockfish descended and remained on the sea-

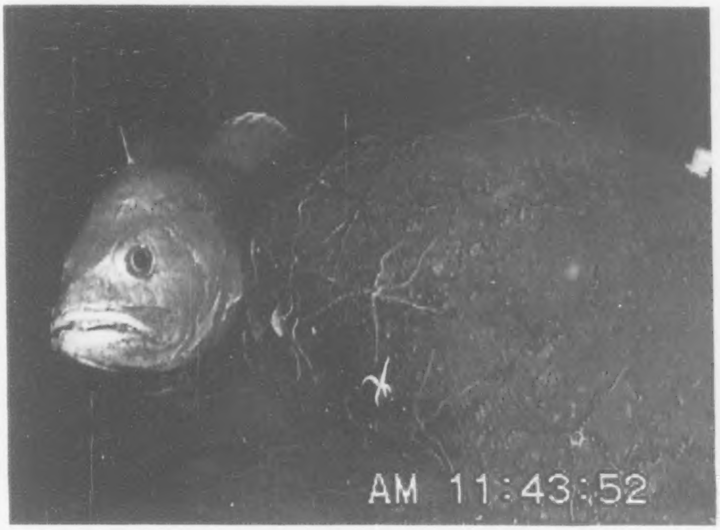

Figure 4

Observation from a submersible of a shortraker or rougheye rockfish lying against a boulder in the eastern Gulf of Alaska in May 1992.

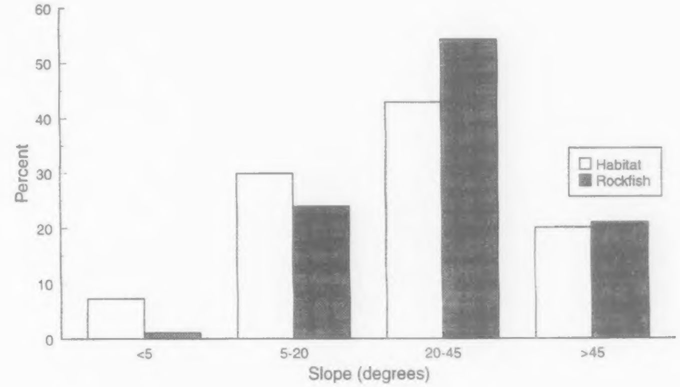

Figure 5

Four levels of slope observed on the seafloor, and the percent occurrence of habitat and percent occurrence of shortraker and rougheye rockfish associated with each level. Observations are from a submersible in the eastern Gulf of Alaska, 1992.

floor in response to the submersible. However, some above-bottom rockfish may not be captured because of their slow rates of descent. Bottom-trawl assessment gear is not designed to sample the steep-slope, boulder habitats occupied by these species, and the few trawl hauls that are completed in boulder habitat likely do not sample rockfish associated with boulders. An assessment method is needed that addresses the wide range of habitats, above-bottom distribution, and grouping behavior of shortraker and rougheye rockfish. Longline gear and bottom trawls with large rollers can sample rugged habitat, and studies are currently underway to determine the efficiency of these gears for sampling shortraker and rougheye rockfish.

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Abstract.–Concentrations of lipids and protein were measured in embryos during gestation in two species of viviparous rockfishes off the central California coast. Total lipids and protein declined linearly through embryonic maturation in semipelagic yellowtail rockfish, *Sebastes flavidus*, and pelagic shortbelly rockfish, *Sebastes jordani*. Energetically, lipids were the predominant source of energy for embryonic development in both species, but lipid and protein catabolism was significantly greater for yellowtail rockfish. Total lipids, protein, and lipid class composition were measured during embryonic maturation in three populations of shortbelly rockfish, located at Ascension, Pioneer, and Bodega submarine canyons, to determine intraspecific variability of nutritional dynamics. Triacylglycerols and polar lipids (mostly phospholipids), the predominant lipid classes in all maturation stages, were depleted through embryonic development. Steryl or wax esters and cholesterol also declined, but were in much lower concentrations. The goodness-of-fit of linear regressions for protein, total lipid, and lipid classes by stage of embryonic maturation allowed estimations of their concentrations at birth, thus providing a measure of nutritional condition, or qualitative reproductive success. Analyses determined that there were significant differences in metabolism and estimated concentrations at birth of nutrients between the two species and among the shortbelly rockfish populations, indicating differential potential for survival during early planktonic life stages until favorable feeding conditions occur. Results suggest that the contribution of individual populations to the diversity of metapopulations or year classes may be influenced by the nutritional condition of larvae at birth.

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Nutritional dynamics during embryonic development in the viviparous genus *Sebastes* and their application to the assessment of reproductive success

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Variability of annual recruitment to marine fish stocks has been attributed to several factors, including the quantity and quality of progeny produced and the influences of environmental conditions on subsequent survival. Although either factor could be effective alone, at times they may interact. Poor reproductive success, manifested by low fecundity or unhealthy progeny, or both, occurring at times of unfavorable environmental conditions, may lead to particularly weak year classes. There is evidence that factors operating at or near the time of spawning affect year-class strength in rockfishes (genus *Sebastes*) along the west coast of North America. Year-class failures of two species of rockfish were found at the extremes of the physical environmental spectrum off the central coast of California during years of very low or very high upwelling (Ralston and Howard, 1995). The data from that investigation suggested that year-class strength of yellowtail rockfish (*Sebastes flavidus)* and blue rockfish (*Sebastes mystinus*) was related to environmental conditions and was established before the pelagic juvenile stage. Further, annual variation in fecundity does not appear to be great enough to account for the variation seen in fishery recruitment of yellowtail rockfish (Eldridge and Jarvis, 1995) or other species (Shepherd and Cushing, 1980). Thus, maternal processes contributing to the health or fitness of embryos or early larvae, in addition to the more often assessed environmental factors, may significantly influence survival and year-class strength.

The assessment of reproductive success includes the determination of both the quantity and quality of progeny because year-class strength may be influenced by the health of newborns as well as by the number produced. Although fecundity is often used as a measure of reproductive success and has been related to biological and environmental factors (Blaxter, 1969), less attention has been given to the assessment of the qualitative aspects of reproductive success. This is due, in part, to the difficulty of determining which variables or processes are valid measures of egg, embryo, or larval health. Various measures have been proposed, such as egg size (Blaxter and Hempel, 1963), histological criteria (Theilacker, 1978), and biochemical analyses, including nucleic acids (Buckley, 1984), enzyme activity (Clarke et al., 1992), and biochemical composition (reviewed by Ferron and Leggett, 1994). All have merits; however, factors such as the degree of relationship to growth or survival potential, ease or cost of analysis (or both), operational feasibility, or the ability to assess adequate numbers of replicates for statistical validity often diminish their utility in routine assessments of reproductive success. Consideration of when, during egg and embryonic development, valid estimates can be made is also critical to accurate assessment of success. Ideally, evaluation at hatching or birth would provide the most accurate determination of health and survival potential, but this event is of very short duration, and obtaining enough individuals to characterize a population or species is difficult.

The nutritional status, or energy content, of embryos and larvae has a clear relationship to growth and survival potential because the amount of metabolically available energy establishes the duration of survival in the environment until adequate food becomes available. Starvation during the early stages of development has been considered a major source of mortality or reduced fitness and may contribute to fluctuations in year-class strength (May, 1974; Shepherd and Cushing, 1980; Rissik and Suthers, 1996).

Low and unstable abundance of prey typifies the environment off central California during winter and early spring (Ainley et al., 1993), the period when many species of viviparous rockfish give birth (Wyllie Echeverria, 1987). Pelagic larvae rely on endogenous nutritional reserves to supplement sparse forage until the biologically productive annual upwelling season begins, usually in late March or April (Bakun, 1975).

This study describes protein and lipid metabolism during embryonic development in two species of the viviparous genus *Sebastes*. A procedure is presented to estimate the lipid and protein composition at parturition, or birth, which provides a measure of nutritional status and thus may be related to the probability for survival at the earliest free-living stage. Nutritional status at birth is presented for yellowtail rockfish and three populations of shortbelly rockfish (*Sebastes jordani*), thereby providing comparisons between congeners occupying different ecological niches and among populations separated spatially. These data are the first documentation of lipid class composition in eggs, embryos, and larvae of a viviparous marine teleost.

Materials and methods

Female *S. flavidus* and *S. jordani* were obtained from January to March, the period of reproductive development spanning late vitellogenesis to parturition, at locations off the central California coast. Yellowtail rockfish were captured by hook-and-line at Cordell Bank (38°01'N 123°25'W), a marine bank 37 km west of Pt. Reyes, at depths ranging from 50 to 150 m. Shortbelly rockfish were collected by trawl at 150 to 200 m depth in the proximity of three submarine canyons: Bodega Canyon (ca. 38°13'N 123°22'W), Pioneer Canyon (ca. 37°24'N 122°52'W), and Ascension Canyon (ca. 37°01'N 122°25'W). Fish were held on ice for up to 12 h until examination. Morphometrics (e.g. standard length; body and liver weight) were recorded and ovaries excised, weighed, and stored at –70°C. The stage of oocyte or embryonic development was identified by microscopy according to the classification scheme of Yamada and Kusakari (1991) for *Sebastes schlegeli* (Table 1).

Table 1

Embryo maturation stages (EMS) in *Sebastes flavidus* and *Sebastes jordani*.

EMS	Description
1	Late vitellogenic or migratory nucleus oocyte
2	Formation of germ disc
3	2-celled
4	4-celled
5	8-celled
6	16-celled
7	32-celled
8	64-celled
9	Morula
10	Early blastula
11	Late blastula
12	Beginning of epiboly
13	Early gastrula
14	Late gastrula
15	Embryonic shield
16	Head fold
17	Optic vesicles
18	Somite formation begins
19	Finfold
20	Optic cups
21	Auditory placodes
22	Lens forms
23	Otoliths
24	Pectoral fins
25	Retinal pigmentation
26	Heart pumping
27	Lens transparent
28	Mouth and anus open
29	Peritoneum pigmented
30	Yolk reduction
31	Prehatching
32	Hatching
33	Hatched, preborn larva

Lipids were extracted from oocytes and embryos by the method of Bligh and Dyer (1959). Total lipids were quantified by using thin layer chromatography with flame ionization detection (TLC-FID) by an Iatroscan TH-10 Mark III (MacFarlane et al., 1990; MacFarlane et al., 1993). Lipids were separated into steryl or wax ester, triacylglycerol, nonesterified fatty acid, cholesterol, and polar lipid classes on Chromarods S-III in a solvent bath of hexane:ethyl ether:formic acid at a ratio of 246:54:0.09. Quantification of separated peaks by TLC-FID was accomplished by comparing peak areas to external standard curves for each lipid class. Cholesterol oleate, triolein, oleic acid, cholesterol, and phosphatidylcholine, purchased from Sigma Chemical Co. (St. Louis, MO), were used as standards. Total protein was estimated with the Lowry method by using a bovine serum albumin standard (Lowry et al., 1951).

Analysis of variance (ANOVA) was employed to assess variation in lipids and protein by embryo maturation stage (EMS), rockfish species, or population of shortbelly rockfish. Estimated concentrations of nutrients at parturition were obtained by linear regression. All analyses were performed with SAS statistical software (SAS Institute, Inc., 1989).

Lipids and protein data are presented as concentrations, mg/g wet weight. Changes in concentration during embryonic development represent absolute changes in the quantities of lipids and protein because ovarian mass remained statistically constant through gestation for both species. ANOVA results of the relationship between GSI [gonadosomatic index = (ovary weight/body weight) × 100] and EMS were $P = 0.242$ (F=1.396, df=59) for yellowtail rockfish and $P = 0.622$ (F=0.243, df=202) for shortbelly rockfish. During gestation, changes in organic mass of ovaries were compensated by changes in water concentration. Regression equations for ovarian water concentration by EMS were

Yellowtail rockfish ovarian water (mg/g)
= 608.5 + 8.292(*EMS*),
[df=59, F=203.7, P<0.0001, r^2=0.778]

Shortbelly rockfish ovarian water (mg/g)
= 655.2 + 6.860(*EMS*).
[df=172, F=782.6, P<0.0001, r^2=0.821]

Results and discussion

There was a progressive decline in total lipid and protein during embryogenesis in yellowtail rockfish, *Sebastes flavidus* (Fig. 1). The concentration of total lipid decreased from a mean of 149.8 mg/g in unfertilized, late vitellogenic oocytes (EMS 1) to an estimated concentration of 48.4 mg/g for fully formed, hatched larvae (EMS 33) at parturition. Although no pregnant females were caught with embryos at EMS 33, the goodness-of-fit (r^2 value) of the linear regression of lipid concentration on embryo maturation stage (Table 2) suggested that calculation of total lipid at parturition was valid (Table 3). Similarly, protein declined from 225.9 mg/g during EMS 1 to 52.1 mg/g at EMS 33 (Fig. 1; Table 3). These data indicate that yellowtail rockfish embryogenesis consumed more protein than lipid for nutritional requirements because protein concentration declined 77% during development whereas total lipids decreased 68%. From an energetic perspective, however, lipid was predominantly utilized. Using values for physiologically available energy density of 39.6 kJ/g of lipid and 20.1 kJ/g of protein (Brett and Groves, 1979), we found that the 101.4 mg lipid/g embryo depleted during embryogenesis yielded 4.02 kJ of energy, whereas the 173.8 mg protein/g embryo yielded 3.49 kJ. The predominance of lipid as an energy source for viviparous reproductive development in yellowtail rockfish has been demonstrated previously (MacFarlane et al., 1993; Norton and MacFarlane, 1995). The consumption of yolk proteins, particularly those with high molecular weights > 70 kDa, during embryonic maturation of yellowtail rock-

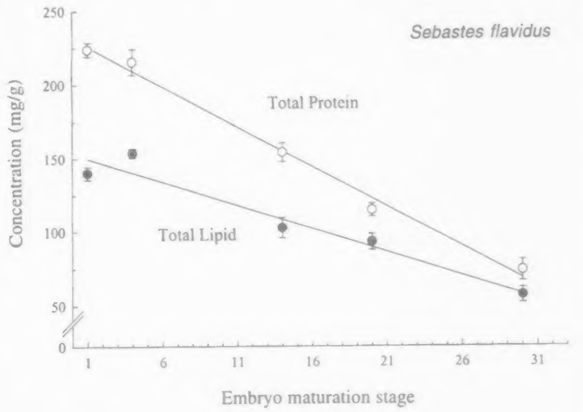

Figure 1

Total lipid and protein concentrations in oocytes and embryos by embryo maturation stage (EMS) in female yellowtail rockfish, *Sebastes flavidus*, from prefertilized oocytes (EMS 1) through the yolk-reduction stage (EMS 30). Data presented as means ± SE. Mean number (range) of females assayed at each EMS was 12 (9–17). See Table 1 for descriptions of EMS.

Table 2

Linear regression parameter estimates for mean protein and lipid concentrations in rockfish embryos in relation to embryo maturation stage (EMS). Data are for yellowtail rockfish (*Sebastes flavidus*) and three populations of shortbelly rockfish (*Sebastes jordani*) from Ascension, Pioneer, and Bodega Canyons. ND = below detection (<0.3 µg); NS = $P > 0.05$. TAG = triacylglycerols; NEFA = nonesterified fatty acids; CH = cholesterol; PL = polar lipids.

Variable	r^2	Intercept ±SE	*P*	Slope ±SE	*P*
S. flavidus (*n*=60)					
Total lipid	0.946	153.0 ± 7.6	<0.001	–3.17 ± 0.44	<0.005
Total protein	0.993	231.3 ± 4.6	<0.0001	–5.43 ± 0.27	<0.001
S. jordani					
All canyons (*n*=212)					
Total lipid	0.884	89.4 ± 3.8	<0.0001	–1.86 ± 0.17	<0.0001
Total protein	0.895	167.8 ± 6.0	<0.0001	–2.85 ± 0.27	<0.0001
Esters	0.695	7.4 ± 0.5	<0.0001	–0.17 ± 0.02	<0.0001
TAG	0.917	43.0 ± 1.7	<0.0001	–0.98 ± 0.08	<0.0001
NEFA	0.141	–0.1± 0.1	NS	0.01 ± 0.00	NS
CH	0.639	3.8 ± 0.2	<0.0001	–0.05 ± 0.01	<0.0001
PL	0.889	35.4 ± 1.4	<0.0001	–0.66 ± 0.06	<0.0001
Bodega Canyon (*n*=49)					
Total lipid	0.699	81.0 ± 6.9	<0.0001	–1.54 ± 0.32	<0.001
Total protein	0.676	174.1 ± 14.9	<0.0001	–3.17 ± 0.69	<0.001
Esters	0.750	7.3 ± 0.6	<0.0001	–0.16 ± 0.03	<0.0001
TAG	0.704	37.4 ± 3.5	<0.0001	–0.80 ± 0.16	<0.0001
NEFA	ND	ND	ND	ND	ND
CH	0.503	3.4 ± 0.3	<0.0001	–0.04 ± 0.01	<0.01
PL	0.665	32.8 ± 2.6	<0.0001	–0.54 ± 0.12	<0.001
Pioneer Canyon (*n*=102)					
Total lipid	0.844	88.3 ± 4.2	<0.0001	–1.97 ± 0.18	<0.0001
Total protein	0.714	177.0 ±10.8	<0.0001	–3.29 ± 0.46	<0.0001
Esters	0.766	7.4 ± 0.5	<0.0001	–0.18 ± 0.02	<0.0001
TAG	0.835	44.6 ± 2.5	<0.0001	–1.12 ± 0.11	<0.0001
NEFA	0.284	–0.2 ± 0.1	NS	0.01 ± 0.00	<0.01
CH	0.719	3.9 ± 0.2	<0.0001	–0.06 ± 0.01	<0.001
PL	0.838	32.7 ± 1.4	<0.0001	–0.62 ± 0.06	<0.0001
Ascension Canyon (*n*=61)					
Total lipid	0.419	90.4 ± 8.0	<0.0001	–1.36 ± 0.41	<0.005
Total protein	0.451	165.1 ±11.8	<0.0001	–1.93 ± 0.59	<0.005
Esters	0.227	7.2 ± 1.0	<0.0001	–0.11 ± 0.05	<0.05
TAG	0.348	42.4 ± 4.6	<0.0001	–0.68 ± 0.24	<0.01
NEFA	0.072	0.1 ± 0.1	NS	0.00 ± 0.00	NS
CH	0.257	3.8 ± 0.3	<0.0001	–0.03 ± 0.01	<0.05
PL	0.520	36.9 ± 2.6	<0.0001	–0.55 ± 0.14	<0.001

fish has also been reported (MacFarlane and Bowers, 1995). Calculations of lipid and protein utilization for embryogenesis in yellowtail rockfish represent net consumption and conservative estimates because at least some maternal contributions to embryo development occur during gestation (MacFarlane and Bowers, 1995). Radio-labelled phosphatidylcholine injected into the circulatory system of pregnant females resulted in radioactivity in embryos, indicating matrotrophy for this phospholipid. The extent to which matrotrophy exists for other lipids and protein is unknown.

As in yellowtail rockfish, total lipid and protein concentrations declined linearly according to stage of development in embryos of shortbelly rockfish, *Sebastes jordani* (Fig. 2).

Embryonic development consumed 55% of the protein and 68% of the total lipid present at fertilization. Thus, both species of rockfish metabolized the same proportion of total lipids, whereas protein was conserved in shortbelly rockfish in relation to yellowtail rockfish embryogenesis. It should be noted, however, that yellowtail rockfish had significantly greater protein resources for embryogenesis at fer-

Table 3

Estimated concentrations of lipids and protein in *Sebastes flavidus* and *Sebastes jordani* larvae at birth. *S. jordani* data are for all populations combined and for each of three populations at Bodega, Pioneer, and Ascension submarine canyons. Values presented as mean ± SD in mg/g wet weight. TAG = triacylglycerols; NEFA = nonesterified fatty acids; CH = cholesterol; PL = polar lipids.

		Sebastes jordani			
Variable	*Sebastes flavidus*	All	Bodega	Pioneer	Ascension
Protein	52.1 ± 5.2	73.6 ± 6.4[1]	69.3 ±10.2	68.5 ± 6.3	101.3 ± 9.1[4]
Total lipid	48.4 ± 8.5	28.1 ± 3.7[2]	29.4 ± 4.7[3]	23.3 ± 2.7	45.7 ± 6.4[4]
Esters	—	1.9 ± 0.4	1.9 ± 0.4[3]	1.4 ± 0.3	3.8 ± 0.7[4]
TAG	—	10.5 ± 2.0	11.0 ± 2.4[3]	7.6 ± 1.6	20.1 ± 3.7[4]
NEFA	—	0.1 ± 0.1	—	0.2 ± 0.0	0.0 ± 0.1
CH	—	2.1 ± 0.1	2.0 ± 0.2	2.0 ± 0.1	2.9 ± 0.2[4]
PL	—	13.6 ± 1.4	14.5 ± 1.8[3]	12.1 ± 0.9	18.9 ± 2.1[4]

[1] Significantly greater than that for *S. flavidus* ($P<0.0001$).
[2] Significantly less than that for *S. flavidus* ($P<0.01$).
[3] Greater than that for *S. jordani* at Pioneer Canyon ($P<0.001$).
[4] Greater than that for *S. jordani* at Bodega and Pioneer Canyons ($P<0.0001$).

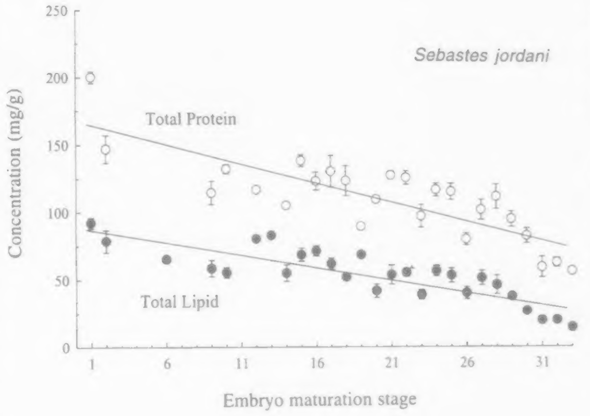

Figure 2

Total lipid and protein concentrations in oocytes and embryos in female shortbelly rockfish, *Sebastes jordani*, from prefertilized oocytes (EMS 1) through the hatched preborn larval stage (EMS 33). Data (means ± SE) from shortbelly rockfish from populations at all three submarine canyons are shown. Mean number (range) of females assayed at each EMS was 8 (1–21). See Table 1 for description of EMS.

tilization than did shortbelly rockfish, 225.9 mg/g compared with 165.0 mg/g (Table 2). At birth, the estimated concentration of protein in shortbellly rockfish larvae was significantly greater than that in newborn yellowtail rockfish ($P<0.0001$); however, the total lipid concentration was less ($P<0.01$) (Table 3). That shortbelly rockfish have less lipid at parturition suggests they have a greater urgency for feeding than yellowtail rockfish soon after birth, or else catabolism of tissue protein would be required for maintenance, reducing the probability of survival.

Energetically, lipid was the predominant fuel for embryo development for shortbelly rockfish, as for yellowtail rockfish. The 59.4 mg lipid/g embryo metabolized between fertilization and parturition represented 2.35 kJ/g, and the 91.3 mg protein/g embryo represented 1.84 kJ/g.

Total energy consumed for embryogenesis was significantly greater in yellowtail rockfish than in shortbelly rockfish ($P<0.0001$). The production of a gram of fully formed, hatched, preborn larval yellowtail rockfish required the expenditure of 7.51 kJ of energy. For shortbelly rockfish, the equivalent energetic cost was 4.19 kJ/g of EMS-33 larvae. Because the average weight of ovaries at late stages of gestation was 204.9 ± 16.9 g ($n=17$) in yellowtail rockfish but only 43.4 ± 2.8 g ($n=21$) in shortbelly rockfish, requirements for maternally supplied nutrients were much greater for yellowtail rockfish. For comparison, the mean standard length and total weight for female yellowtail rockfish was 36 ± 0.5 cm and 1304 ± 55 g versus 21 ± 0.2 cm and 150 ± 4 g for the shortbelly rockfish assessed in this study.

The significant difference in energy required to produce a gram of larvae in the hatched, preborn stage in the two rockfish species may relate to differences in reproductive strategy. Yellowtail rockfish produce about 700,000 eggs/female (Eldridge and Jarvis, 1995) whereas shortbelly rockfish fecundity is about 16,500 eggs/female (Eldridge[1]). Also, yellowtail rockfish eggs and hatched larvae are considerably smaller than those of shortbelly rockfish (Matarese et al., 1989; Eldridge[1]). Greater energy consumption for production of yellowtail rockfish larvae may be a consequence of greater energy required for the synthesis of more larvae, their organelles, and subsequent cellular differentiation.

The relative importance of lipids and protein as sources of nutrition during embryonic and larval development in oviparous fishes has been presented in other reports. In the marine teleost, *Sparus aurata*, free amino acids were the main source of energy during the relatively short embryonic period (ca. 51–58 h postfertilization) whereas lipids and protein did not supply substantial energy until after hatching (Rønnestad et al., 1994). Winter flounder (*Pseudopleuronectes americanus*), by contrast, used small amounts of carbohydrate first, then protein until hatching (Cetta and Capuzzo, 1982). Lipid depletion did not occur until after hatching. Protein concentrations were stable, whereas lipids were catabolized in eggs and newly hatched larvae of Senegal sole (*Solea senegalensis*) (Mourente and Vasquez, 1996). According to these researchers, this pattern of lipid metabolism is characteristic of temperate marine fishes with eggs containing oil globules, high lipid content, and short developmental periods. The rockfish species in the present study are temperate marine teleosts that contain oil globules and high lipid levels. However, they are viviparous and have relatively lengthy development, yet catabolize both protein and lipids for energy-consuming processes, thus emphasizing the great variability and lack of generality in the sources and patterns of nutrient use for embryonic and larval development in fishes.

Total lipid concentrations can be considered a measure of physiological condition of larvae (Ferron and Leggett, 1994), and thus an indicator of potential reproductive success, but not all types, or classes, of lipids are equivalent with respect to metabolic availability or *in vivo* energy yield. Therefore, fractionation of total lipids into classes representative of energy-yielding and structural functions provides greater knowledge of the amount of energy available to sustain growth and survival once the larvae are released into the environment.

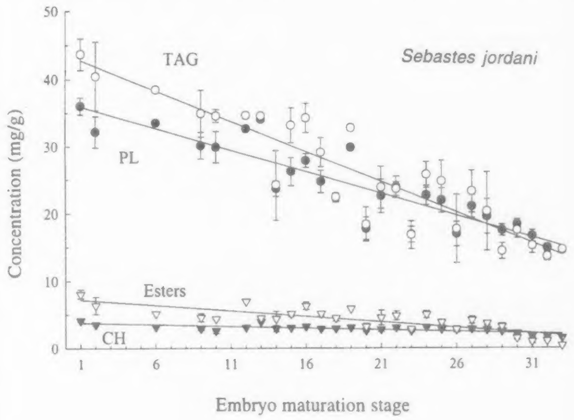

Figure 3

Changes in lipid classes during embryonic maturation in shortbelly rockfish, *Sebastes jordani*. Data (means ± SE) are from populations at all three submarine canyons. Number of females assayed for each EMS is same as in Figure 2. See Table 1 for description of EMS.

Total lipid from shortbelly rockfish embryos was fractionated into five lipid classes: steryl/wax esters (esters), triacylglycerols (TAGs), nonesterified fatty acids (NEFAs), cholesterol (CH), and polar lipids (PLs). The separations were not performed on yellowtail rockfish embryos owing to loss of samples before chromatographic analysis.

Triacylglycerols (TAGs) and PLs were the predominant lipids in all stages of embryonic maturation and showed the greatest declines during development (Fig. 3). Cholesterol (CH) and esters were found in much lower concentrations and declined slightly, but significantly, during embryogenesis (Fig. 3; Table 2). Nonesterified fatty acids (NEFAs) were found in very low concentrations and did not vary significantly by stage of maturation (Table 2).

The depletion of TAG and PL from fertilization to birth indicates the oxidation of these lipid classes for energy-requiring embryogenic processes. The use of TAG for energy storage and fuel during embryonic and larval development is well known in fishes (Boulekbache, 1981; Vetter et al., 1983; Tocher and Sargent, 1984; Fraser, 1989). Polar lipids, consisting mainly of phospholipids, such as phosphatidylcholine and phosphatidylethanolamine, although used as fundamental structural units of all biological membranes, have been shown to be a significant source of energy also for embryonic development in other fishes (Sargent, 1995). The relative contribution of TAG and PL to the energy demands of embryonic development varies by species. Whereas in cod (*Gadus morhua*) (Fraser et al., 1988; Finn et al., 1995) and Atlantic herring (*Clupea harengus*) (Tocher et al., 1985) PL was the major source of energy, in Senegal sole (Mourente and Vasquez, 1996) and gilthead sea bream (Rønnestad et al., 1994), TAG was primarily catabolized. In Atlantic salmon (*Salmo salar*), the PL phosphatidylcholine and TAG were used equally to meet energy requirements (Cowey et al., 1985).

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[1] Eldrige. M. B. 1997. Tiburon Laboratory, Southwest Fisheries Science Center, 3150 Paradise Drive, Tiburon, CA 94720. Unpubl. data.

The changes in lipid composition during embryogenesis in yellowtail and shortbelly rockfishes described here represent the first data of this kind for rockfishes or any viviparous marine teleost. The use of PL as a primary source of energy may be consistent with results from previous research revealing that phosphatidylcholine was supplied to developing embryos of yellowtail rockfish from maternal sources both before and during development (MacFarlane and Bowers, 1995). Perhaps the facility to supply phospholipids matrotrophically enhances their use as energy-yielding substrates. High concentrations of TAG in prefertilized eggs (EMS 1) and its importance as an energy source are not unexpected because both species feed heavily on euphausiids (Brodeur and Pearcy, 1984), which contain large amounts of TAG (Fricke and Oehlenschläger, 1982).

Lipid class composition has been promoted as a measure of nutritional condition for larvae of a variety of oviparous marine fish, including Atlantic cod (Lochmann et al., 1995), Atlantic herring (Fraser et al., 1987), and anchovy *Engraulis mordax* (Håkanson, 1989). Depending upon the species, the quantities of TAG or PL, or both, related to the probability for survival. Lochmann et al. (1995) suggested that survival was related to a condition index based on a discriminant function of TAG, PL, and defatted dry weight in laboratory and field-collected cod larvae. Triacylglycerol (TAG) was regarded as the critical variable in condition for herring (Fraser et al., 1987) and anchovies (Håkanson, 1989).

It is reasonable to apply this concept to the assessment of larvae from viviparous species as well. The nutritional status of larvae just prior to parturition would represent their condition at the start of life in the marine environment and would be related to their ability to survive until adequate feeding occurs. The presence of an oil globule in rockfish larvae during the early days after birth argues for the importance of lipids for energy. For rockfish, the amounts of TAG at birth should be related to survival potential because this lipid class is the predominant component in oil globules of most fishes (Henderson and Tocher, 1987; Heming and Buddington, 1988) and has consistently been shown to correlate with physiological condition (Fraser, 1989).

We analyzed embryos in pregnant female shortbelly rockfish from populations living in the proximity of three submarine canyons off the central California coast. The purpose was to determine the variability in metabolism of lipid classes for specific populations and the estimated concentrations of each lipid class at birth, thus providing a measure of nutritional status and relative probability for survival. When lipid class concentrations were assessed in embryos from the separate populations, there were differences in the amounts and rates of depletion during intraovarian development (Table 2). Two-way ANOVA determined there were significant differences among populations at the three canyons, despite being located within about a one-degree latitude span off the central California coast. All lipid classes, except NEFA, varied significantly by EMS ($P<0.0001$), population ($P<0.0001$), and the interaction of population and EMS ($P\leq0.05$).

The changes in concentrations of lipid classes were linearly related to EMS for embryos from each population (Table 2). Parameter estimates from linear regressions of each lipid class by stage of embryonic maturation revealed that rates of metabolism differed among the populations (Table 2). The greatest catabolic rates of TAG and PL were found in embryos from the Pioneer Canyon population. Rates of protein depletion were also greater in embryos from Pioneer Canyon and lowest in those from Ascension Canyon.

In conjunction with initial concentrations of protein and lipid classes at fertilization, the rates of nutrient metabolism can be used to estimate concentrations at parturition (EMS 33). The greater rates of nutrient utilization for embryos in females from the population at Pioneer Canyon resulted in the lowest levels of nutritional stores at birth of the three populations evaluated (Table 3). Conversely, newborn larvae from females at Ascension Canyon contained the greatest concentrations of lipids and protein, suggesting that they have a greater likelihood of survival until suitable feeding conditions exist.

The differential status of nutrient levels in larvae at birth may contribute to differences in survival rate among the populations and, thus, influence the diversity of the species year class. Parturition occurs during the winter when oceanic conditions prevail along the California coast. This is the period of lowest primary and secondary productivity annually (Ainley, 1990). Until marine conditions become favorable for biological productivity, usually in April when seasonal upwelling and increasing solar radiation stimulate phytoplankton growth, larvae must subsist on the combined resources of endogenous reserves and limited prey abundance. During the days following birth, the quantity of lipid reserves may influence the length of time larvae can persist until adequate forage is available to sustain survival and growth. Starvation has been considered a factor in recruitment variability in rockfish species (Moser and Boehlert, 1991). Larvae from populations with lesser energy reserves may experience greater mortality, thereby reducing their representation in the year class for the species along the entire coast.

The use of lipid and protein data as an indicator of nutritional condition at birth for rockfish in the genus *Sebastes* marks an extension of such data to viviparous fishes for the first time. Previously, lipid class analyses have been employed for condition assessments only in oviparous fish embryos (Tocher et al., 1985; Fraser et al., 1988) and larvae (Fraser, 1989; Håkanson, 1989; Lochmann et al., 1995).

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Metabolic rate in relation to temperature and swimming speed, and the cost of filter feeding in Atlantic menhaden, *Brevoortia tyrannus*

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Abstract.–Respiration rates of nonfeeding adult menhaden induced to swim against currents of various speeds in a large circular flume at 10°, 15°, and 20°C were measured in order to quantify the cost of swimming separately from total metabolic expenditure during filter feeding. Standard metabolic rates of 0.040, 0.073, and 0.087 mg O_2/(g wet wt · h) at 10°C, 15°C, and 20°C were estimated by extrapolation of the relationship of swimming speed and metabolic rate to zero swimming speed. We determined that when menhaden filter-feed at 20°C, at the preferred swimming speed of 41.3 cm/s, filtering and specific dynamic action (SDA) account for 59% of total energetic expenditures. The cost of locomotion was only about 23% of the total expenditure. Our results are compared with routine oxygen consumption rates of larval and juvenile menhaden as a function of temperature and with extensive metabolic data for sockeye salmon.

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The Atlantic menhaden, *Brevoortia tyrannus,* is a pelagic filter-feeding clupeoid inhabiting coastal waters of North America from Maine to Florida. Menhaden adopt filter feeding in early juvenile life (Peck, 1893; June and Carlson, 1971; Friedland et al., 1984). Adults are obligate filter feeders and consume phytoplankton, zooplankton, and detritus larger than about 13 µm (Durbin and Durbin, 1975). Menhaden are size selective in their feeding, but the basis of selection is passive, reflecting the size distribution of particulate material in the water relative to the "pore size" of the gill rakers; they do not actively pursue individual prey. Energy expenditures during "ram" filter feeding (analogous to towing a plankton net) are high (Durbin et al., 1981; Sanderson and Cech, 1992), probably due to the hydrodynamic drag of the filtering apparatus. However, menhaden compensate for the high cost of filter feeding by regulating their swimming speed to maximize the ratio of net energy gain to expenditure (Durbin and Durbin, 1983), as predicted by Ware (1975). Our study was undertaken to partition the previously determined energetic cost of filter feeding (Durbin and Durbin, 1983) into two components: the cost of locomotion alone and the cost of filter feeding. This division was accomplished by measuring respiration rates of nonfeeding fish forced to swim against currents of known speed and by comparing these respiration rates with those of feeding fish.

Materials and methods

Live Atlantic menhaden, *Brevoortia tyrannis*, were collected from a commercial fish trap located in the lower West Passage of Narragansett Bay on 22 and 25 September 1989. The fish were removed from the trap with dip nets and placed in 114-L seawater-filled polyethylene garbage cans for transport to the Narragansett Bay Campus. Menhaden were randomly divided and placed with three open-flow circular fiberglass tanks, 1.7 m in diameter and 0.5 m deep, supplied with sand-filtered seawater. Acclimation to the three test temperatures (10°, 15°, and 20°C) began 5 October 1989, starting from the ambient temperature, 18°C, with a rate of change of about 1°C/d. Ambient salinities varied between 28 and 30 ppt. The fish were considered acclimated after maintenance for 30 days at the target temperature. Menhaden were fed salmon starter mash (Ziegler Bros., Inc.) at a rate of about 4.5% of dry food:live

Table 1

Vital statistics for the experimental fish are given in the upper panel. Relationships between respiration rate (R, mg O_2/(g wet wt · h)) and swimming speed (S, cm/s or body lengths [BL/s]) are given in the lower panel. T = temperature and FL = fork length, NF = not fed for 24 h, and FF = filter feeding.

T (°C)	No. of fish in sample	FL (cm)	Wet wt (g)	Dry wt (g)
10	13	26.0 ± 0.9	327 ± 45	99.2 ± 15.6
15	13	25.5 ± 0.6	303 ± 38	92.1 ± 15.2
20	10	25.5 ± 1.2	283 ± 40	86.4 ± 12.3

T (°C)	Behavior	Regression equation	r^2	Source
10	NF	$\log_{10} R = 0.0141\ S$ (cm/s) – 1.402 $\log_{10} R = 0.3655\ S$ (BL/s) – 1.598	0.99	This study
15	NF	$\log_{10} R = 0.0095\ S$ (cm/s) – 1.139 $\log_{10} R = 0.2419\ S$ (BL/s) – 1.861	0.90	
20	NF	$\log_{10} R = 0.0086\ S$ (cm/s) – 1.061 $\log_{10} R = 0.2187\ S$ (BL/s) – 1.939	0.96	
20	FF	$\log_{10} R = 0.0271\ S$ (cm/s) – 1.446	0.84	Durbin et al. (1981)

weight/d. The acclimation tanks were cleaned daily. During the holding and experimental periods, a 12 h:12 h light:dark photoperiod was provided by overhead fluorescent lights, and sufficient current was provided to cause the fish to orient head into the current. Experiments took place 3–14 December 1989. Vital statistics for the fish are given in the top section of Table 1.

Respiration measurements were made on a small school of menhaden because studies of schooling fishes have shown that respiration rates are higher and growth rates lower in isolated fish than in those kept in groups (Skazhina, 1975; Kanda and Itazawa, 1978; see also Ross and Backman, 1992). Experiments were begun with the 15°C trials on 3 and 4 Dec., followed by the 10°C trials on 7 and 8 Dec. The 20°C trials were conducted on 14 Dec. Thirteen fish were used for the 10°C and 15°C experiments. For the 20°C trials only 10 fish were used. Digestion is rapid in menhaden (Durbin and Durbin, 1981), and metabolism quickly returns to preceding levels after a meal (Durbin et al., 1981). Thus a starvation period of 24 h was considered sufficient to remove the effect of the previous meal on metabolic-rate measurements. Handling and transfer protocols were similarly chosen to reduce bias due to stress-induced factors, such as those identified by Waring et al. (1992) in flounder and salmon.

A sealed, toroidal fiberglass flume tank (Fig. 1A), modified from Hettler (1976), was used as a respirometer. The flume (2.75 m inside diameter, 0.51 m depth, and 0.39 m wide annular swimming channel) was large enough to hold a small school of adult menhaden. The flume was painted with a white, nontoxic, polyester gel coat. Black radial stripes 5.1 cm wide, spaced 21.8 cm apart (at the inside diameter of the flume), were painted on the walls and bottom of the flume, to provide reference marks for later determination of swimming speeds and to provide visual cues for the fish to sense displacement by the flow. To produce the desired flow rates, a high-pressure, 3.7-kW, multi-stage electric pump (Fig. 1A) was connected to coils of polyethylene tubing (6 mm inside diameter) arrayed along the walls of the flume (Fig. 1B). Discharge holes were punched at an angle of about 45° downstream and 20° downward from the horizontal with a hypodermic needle along the length of tubing to form small jets creating a counterclockwise flow in the flume. A valve placed at the pump outlet (Fig. 1A) controlled the speed of water in the flume. Return water to the pump flowed through a drain line located at the bottom of the tank and thence through a bank of 4 fiber-wound cartridge filters (3 µm). An integral reservoir (12.9-L capacity) was used to replenish sample water removed during experiments. Cooling coils were installed along the inner wall of the flume and around the pump housing (Fig. 1B) to remove heat generated by the pump and to maintain a constant temperature during trials. Water temperature was monitored with a YSI Model 2100 Tele-thermometer.

Flow rates within the flume were measured with a General Oceanics Inc. flowmeter connected to a proprietary digital display. The transducer head was

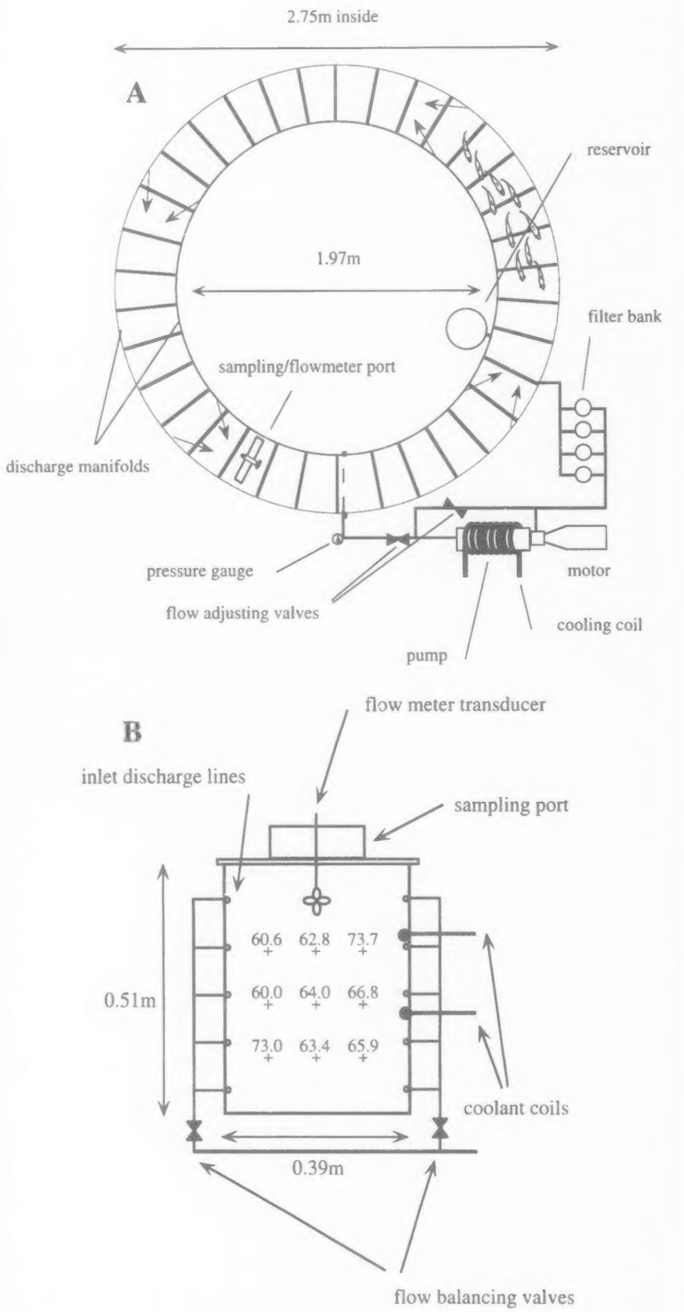
2.75m inside
A
reservoir
1.97m
filter bank
sampling/flowmeter port
discharge manifolds
pressure gauge
motor
flow adjusting valves
cooling coil
pump
flow meter transducer
B
inlet discharge lines
sampling port
60.6
62.8
73.7
60.0
64.0
66.8
0.51m
73.0
63.4
65.9
coolant coils
0.39m
flow balancing valves

Figure 1

(**A**) Schematic view of the toroidal flume respirometer. The direction of flow is indicated by arrows within tank. (**B**) Cross-sectional view of flume tank showing arrangement of water and coolant flow. A typical cross section of the generated flow field is also shown. Speeds are cm/s. The grid spacing is 10.8 cm vertically by 8.3 cm horizontally.

suspended in the flume by a stainless steel rod (Fig. 1B). During experiments the flowmeter head was fixed radially in the middle of the flume, near the top of the water column. However, sensor depth and radial position could be varied to measure flow rate in different regions of the flume. By varying the number of discharge holes across the vertical array of inlet coils and by regulating the flow to the inner and outer inlet coils, it was possible to produce a relatively uniform cross-sectional flow field. Typical flow rates (cm/s) determined at maximum pump pressure (1.38×10^3 kPa), on a grid 10.8 cm vertically by 8.3 cm horizontally measured vertically from the flume bottom, are shown in Figure 1B. Preliminary trials established that the relationship between pressure of the inflowing water from the pump and the flow rate generated inside the flume was linear up to the maximum pump pressure, 1.38×10^3 kPa, corresponding to a flume speed of 64 cm/s. Blank trials without fish demonstrated that the system was airtight and that changes in oxygen concentration due to microbial respiration were negligible over periods comparable to those in the experiments.

Each experiment comprised a series of trials over a 2-d period. Menhaden were anesthetized with MS-222 and transferred to the flume 24 h before an experiment to permit recovery from handling stress (Barton and Schreck, 1987; Waring et al., 1992). The menhaden remained in the flume until the conclusion of the experiment and were fed in the late afternoon of each day. In the morning, fecal material and debris was siphoned off the bottom of the flume, the bottom and interior walls of the flume were scrubbed with a polyethylene scouring pad, and the flume was flushed with filtered seawater. All experiments were conducted during daylight in the afternoon, 24 h after the last feeding. The fish were accustomed to this procedure and quietly circuited the flume. A clear

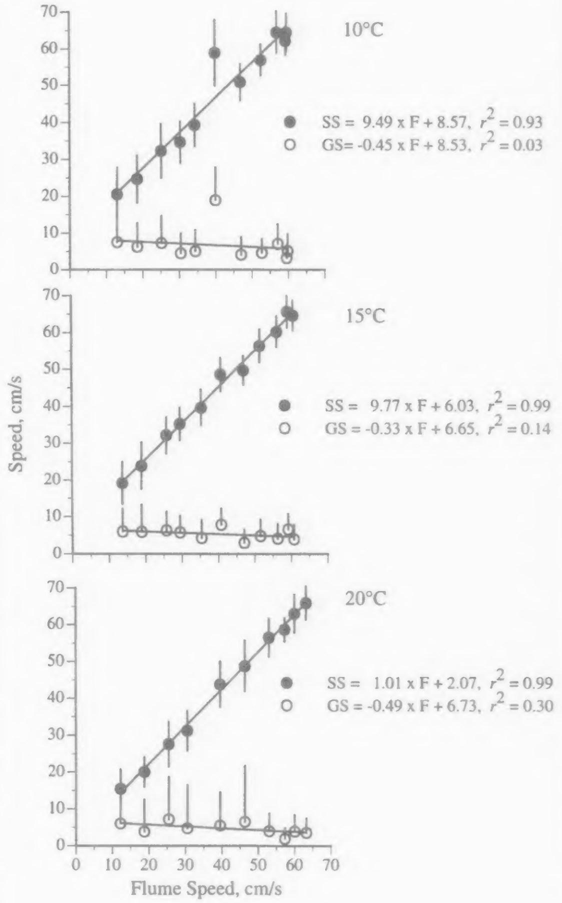

Figure 2

Ground speeds (GS) and true swimming speeds (SS) of Atlantic menhaden, *Brevoortia tyrannus*, swimming against water currents in a toroidal flume respirometer at 10°, 15°, and 20°C. Lower ground speed error bars are not shown.

Plexiglas lid, composed of interlocking sections, was then carefully fitted over the surface of the tank to provide an airtight seal. During respiration trials, the flume was operated as a closed system; between trials and at night, however, the flume received a continuous inflow of temperature-controlled filtered seawater, with a flow rate of about 6 cm/s to orient the fish.

During each 2-d experiment a series of trials was carried out at flume speeds ranging from 12–13 (minimum) to 60–63 (maximum) cm/s. Between four and six trials were conducted per day, with each trial lasting 1 h. Test speeds were selected randomly, and at the completion of a trial the next test speed was set, followed by a 30-min interval during which flow rate became stable again and fish were able to adjust to the new speed. An interval of about 1 h was used to reoxygenate the flume when necessary. Test current speeds were set by regulating the discharge pressure of the circulating pump (Fig. 1A) by using the predetermined pressure to flow-rate calibration curve. Although we attempted to use the same test current speeds at all three temperatures, minor inaccuracies in the calibration curve and gauge readings resulted in only approximately equal test speeds (Fig. 2).

Fish behavior was observed continuously during experiments and recorded with a monochrome MTI Dage M65 video camera suspended directly above the center of the flume and connected to a VHS format video recorder. Swimming speed in relation to the bottom (ground speed, GS) was determined from the video recordings at 3-min intervals, by marking the position of each fish on the video monitor screen with a grease pencil and noting its subsequent location 10 s later. The number of reference marks crossed by each fish during this interval was then multiplied by the distance between marks (21.8 cm) to obtain ground speed. Fish moving upstream were assigned positive values, whereas those swimming downstream were scored negatively. Actual swimming speed (SS) through the water was then computed as the algebraic sum of the ground speed (speed of fish in relation to the bottom) and the flow rate in the flume. Mean swimming speed during a trial was computed from the individual swimming speeds, irrespective of direction.

During experiments a YSI Model 51B dissolved oxygen meter was used to monitor oxygen levels in real time; oxygen content of the water was not permitted to decline below 60% of saturation. At 15-min intervals during a trial, duplicate water samples were siphoned from the collection port into 300-mL biological oxygen demand (BOD) bottles that were allowed to overflow twice their volume and that were then fixed for determination of oxygen content by Winkler titration (Carritt and Carpenter, 1966; Strickland and Parsons, 1972). Analyses were performed on 5–6 50 mL subsamples withdrawn from the bottles with a volumetric pipette. Dissolved oxygen declined linearly over time (overall mean $r^2 \pm 1$ SD for all regressions=0.987 ±0.018). Metabolic rates were therefore assumed to be unaffected by declining oxygen content during the trials. Menhaden respiration rates were computed from the change in dissolved oxygen content over time as determined by least squares linear regression, corrected for the wet weight of the fish and volume of the flume.

Results

The menhaden formed a loose school in the upper central portion of the flume. The fish usually oriented head into the current and moved slowly upstream (positive ground speed). Occasionally a fish would break away and swim downstream with the flow, but within a few seconds reoriented itself to swim against the flow. These brief periods of downstream swimming occurred most frequently at slow current speeds and at the warmest temperature, 20°C. The frequency of occurrence of downstream coasting or swimming during respiration trials was as follows: 0 of 11 trials at 10°C; 2 of 11 at 15°C (2.2% of observations during those 2 trials); and 6 of 10 at 20°C (6.4% of observations in those 6 trials). When corrected for current speed, swimming speeds of fish moving downstream were comparable to those of fish moving upstream. Overall, the incidence of downstream swimming did not significantly affect the results.

In our study, menhaden swimming into a water current maintained a nearly constant ground speed at 10°, 15°, and 20°C (6.8, 5.3, and 4.7 cm/s respectively, or about 0.2 BL/s) (Fig. 2), whereas their true swimming speeds ranged from 20.5 to 64.6 cm/s (10°C), 19.2 to 65.7 cm/s (15°C), and 15.5 to 66.0 cm/s (20°C). The mean ground speed was not significantly different at the three temperatures ($\bar{x} \pm$ SD=6.8 ±5.8 cm/s at 10°C; 5.3 ±4.8 cm/s at 15°C; and 4.7 ±8.2 cm/s at 20°C). Because ground speed remained nearly constant, actual swimming speed increased linearly with increasing current speed in the flume (Fig. 2).

The distribution of individual swimming velocities within the school was unimodal but was skewed towards a speed slightly faster than the flow rate in the flume (Fig. 3). The coefficient of variation in swimming speed declined curvilinearly as velocity increased, indicating that fish behavior grew less variable at higher speeds (Fig. 4). The pattern of decreasing variability with increasing swimming speed was similar at all three temperatures.

Respiration rates increased exponentially with increasing swimming speed (Fig. 5, Table 1). Analysis of covariance revealed that the relationships between respiration rate and swimming speed differed significantly at the three temperatures. The regression slope, or the rate of increase in oxygen consumption per unit swimming speed, was greatest at 10°C, significantly higher than at 15° or 20°C (Fig. 6). The 15° and 20°C curves differed in elevation but not in slope, indicating that the overall level of metabolism was higher at 20°C than at 15°C, but the rate of increase in metabolic rate with increasing swimming speed was similar at the two temperatures. The cost of swimming was therefore higher at 10°C (metabolism increased by a factor of 2.32 per 1 BL increment in swimming speed) than at 15° or 20°C (metabolism increased by 1.75 and 1.65, respectively) (Table 2). At the higher test speeds, metabolic rates at 10°C were equal to or greater than those at 15°and 20° (Fig. 6).

Standard metabolism, as indicated by the *y*-intercepts of the equations given in Table 1, increased with temperature. At 10°, 15°, and 20°C, standard metabolism was equal to 0.040, 0.073, and 0.087 mg O_2/(g wet wt · h) respectively, or 0.131, 0.238, and 0.284 mg O_2/(g dry wt · h). The Q_{10} for standard metabolism (Prosser, 1973) was higher over the interval 10–15°C (3.3) than for 15–20°C (1.4). The Q_{10} over the interval 10–20°C was intermediate (2.2) (Table 3).

Discussion

Previous work has shown that menhaden swimming behavior reflects environmental conditions and food availability. At 20°C, adult menhaden of about 300 g swim at a characteristic speed of about 12.2 cm/s (0.5 BL/s) in still water in the absence of food (Durbin et al., 1981). During feeding, swimming speed and metabolic rate increase hyperbolically with increasing food concentration (Durbin et al., 1981). Hettler (1976) found that routine swimming speed in larval and juvenile menhaden (up to 80 g) increased with temperature but decreased with increasing salinity, starvation, and in the dark.

Ground speeds in the present experiments were remarkably stable considering the tested temperature range and the different energy expenditures at the different current speeds. The decline in individual variability in swimming speed as mean swimming speed increased (Fig. 4) was very similar to that observed by Durbin et al. (1981). This decline in variability may reflect decreased excitability as fish swim faster as well as a transition to steadier swimming with lower energy costs (reviewed in Brett and Groves, 1979; Boisclair and Tang, 1993).

The nearly constant ground speed in all trials indicated that menhaden did not approach their maximum swimming capacity at any of the tested speeds and, as a result, were probably not fatigued at the end of a day's trials despite the lack of rest between trials. The maximum observed metabolic rate of fish in our study, 0.356 mg O_2/(g wet wt · h) at 20°C, while fish were swimming at 63.2 cm/s, was considerably lower than that associated with filter feeding at a slower speed (0.538 mg O_2 /(g wet wt · h) at 20°C and 43.4 cm/s: Durbin et al., 1981), further indicating that the fish were not performing near their physiologi-

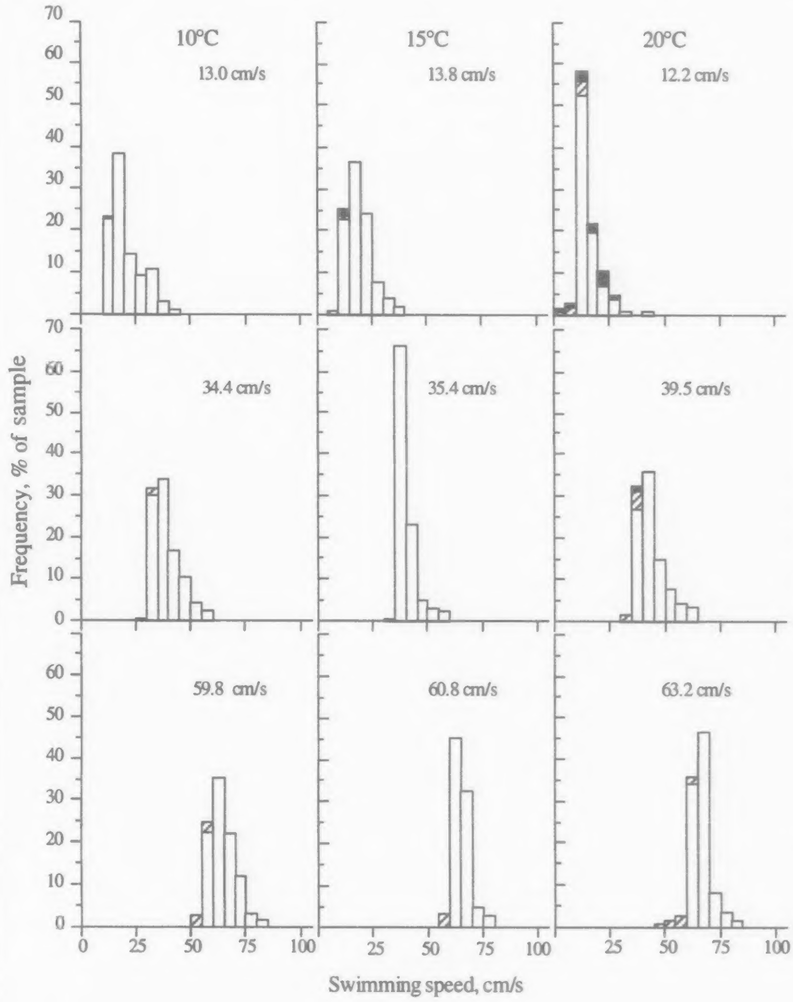

Figure 3

Frequency distribution of swimming speeds within a menhaden school swimming against typical slow, intermediate, and fast flows, at 10°, 15°, and 20°C. The flow rate inside the flume is indicated in each graph. Open bars indicate fish swimming against the current faster than the flume speed; diagonally hatched bars indicate fish swimming against the current, but slower than the flume; solid bars indicate fish actively swimming down current (i.e. with the current).

cal limit in the present experiments. Hettler (1976) measured a high oxygen consumption rate of 0.82 mg O_2/(g wet wt · h) during feeding by juvenile menhaden at 27°C, but the full metabolic scope (Fry, 1957) of menhaden remains unknown. Metabolic scope is related to the surface area of the gills and to the capacity of fish to take up oxygen from the surrounding medium. The unusually large gill area in menhaden (Gray, 1954) suggests that metabolic scope is also large.

We were unable to determine either maximum or critical swimming speeds for adult menhaden (Brett and Glass, 1973) because sufficiently high currents could not be produced in the flume respirometer. Current speeds ranged from 12 to 63 cm/s (0.5 to 2.5 BL/s), which spans the reported range of voluntary swimming speeds during routine activity and feeding (Durbin and Durbin, 1975; Hettler 1976; Durbin et al., 1981). Swimming capacity is unusually high in Atlantic menhaden; Hartwell and Otto (1978) reported that 5.8-cm-SL juvenile menhaden sustained a critical swimming speed of 15.8 BL/s for 64 min at 20°C. The critical swimming speed of similarly sized sockeye salmon at 15°C is about 7 BL/s (Brett and Glass, 1973).

Standard metabolism (Fry, 1957) is a measure of basic maintenance costs and as such may be a useful reference level for interspecific comparisons. The magnitude of standard metabolism also seems to reflect species life styles with respect to their general activity levels. Standard metabolic rates for menhaden (Table 3) were lower than those for active predators like the bluefish, *Pomatomus saltatrix* (0.156 mg O_2/(g wet wt · h), for 217-g fish at 15°C (Freadman, 1979), but higher than those for the sedentary flatfish *Limanda limanda* (0.015, 0.029, and 0.042 mg O_2/(g wet wt · h) at 5°, 10°, and 15°C for 236–400 g fish (Duthie, 1982)). Standard metabolism in menhaden was similar to that of sockeye salmon (Brett, 1964) at 15°C, but lower at 10° and 20°C (Table 3). Durbin et al. (1981) previously estimated standard metabolism for menhaden at 20°C to be only 0.036 mg O_2 /(g wet wt · h), from the regression of feeding metabolism as a function of swimming speed. However we believe that the present higher estimates are more reliable because the data include a broader range of swimming speeds and require less extrapolation to zero swimming speed than the earlier estimate.

The Q_{10} values (Prosser, 1973) provide a measure of the effect of environmental temperature on metabolic rates. The Q_{10} for standard metabolic rate in our study was very close to that of Hettler for routine metabolism in juvenile menhaden (Table 3). The decline in Q_{10} between 10°–15°C and 15°–20°C thus appears to be real. A similar pattern was observed in dab, *Limanda limanda*, where the Q_{10} over 5°–10°C was higher than over 10°–15°C (3.7 and 2.1 respectively (Duthie, 1982). The more extensive data of Hettler (1976) and Brett (1964) indicate that over a wide temperature range (Hettler: 14–24°C; Brett: 5–24°C), the Q_{10} for metabolic rate is close to 2.0, but within this range the Q_{10} declines as the thermal optimum is approached and increases towards the thermal extremes for the species.

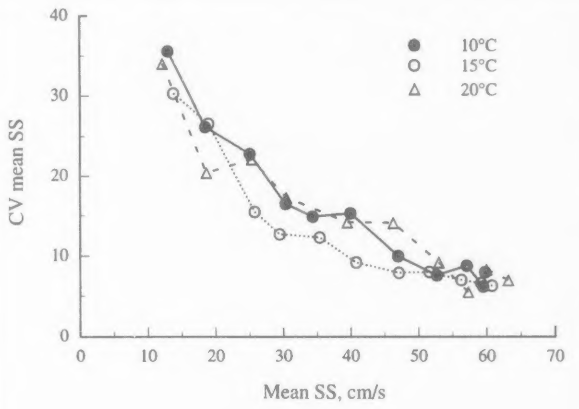

Figure 4

The coefficient of variation (CV) in relation to mean swimming speed (SS) of a menhaden school in the respirometer at 10°, 15°, and 20°C.

Table 2

Comparison of the metabolic cost of increasing swimming speed by 1 BL/sec (ratio of respiration rate at 2BL:1 BL/s) in Atlantic menhaden, *Brevoortia tyrannus* (Table 1, this study), with that in sockeye salmon, *Oncorhynchus nerka* (Table II in Brett, 1964). Fish were not fed for 24 h.

	Menhaden (this study)			Sockeye (Brett, 1964)		
Temp. (°C)	Length (cm)	Wt (g)	Cost	Length (cm)	Wt (g)	Cost
5				18.0	50	2.19
10	26.0	327	2.32	18.0	50	1.91
15	25.5	303	1.75	18.0	50	1.86
20	25.5	283	1.65	18.0	50	1.66
24				18.0	50	1.48

Hettler's data on routine metabolic rate in juvenile menhaden, when extrapolated to 300-g fish (Table 3), yield relatively high routine metabolic rates compared with those observed by Durbin et al. (1981) (0.10 mg O_2/(g wet wt · h) at 20°C). Because the maximum weight of Hettler's fish was only 74.3 g, the extrapolated values for 300-g fish are most likely overestimates. The calculated routine rates in Table 3 correspond to swimming speeds of 18.8, 25.7, and 27.4 cm/s at 10°, 15°, and 20°C, respectively, which were faster than the routine speed of 12.2 cm/s at 20°C reported by Durbin et al. (1981).

Routine metabolic rates are measured directly at spontaneous activity levels. Thus routine rates reflect real world activity levels, because few fish actually sleep or totally cease movement that would depress metabolic rates to basal or standard levels. Our present observations do seem to be comparable

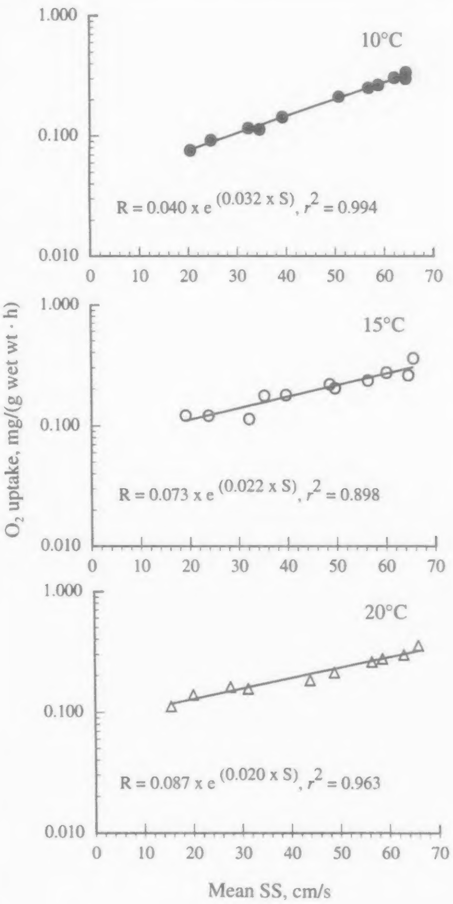

Figure 5

Relation between metabolic rate and swimming speed of fish in the respirometer at 10°, 15°, and 20°C.

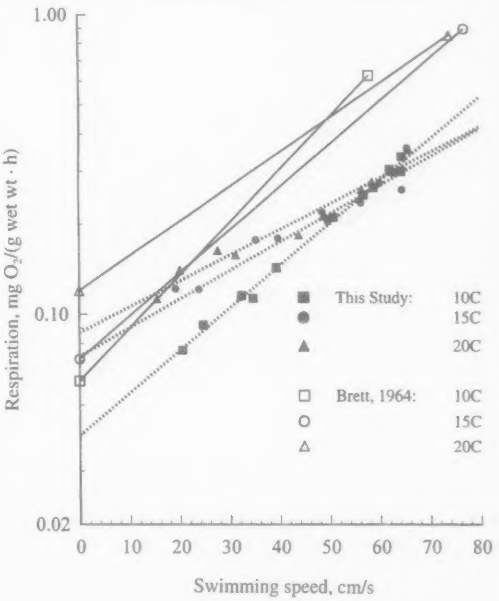

Figure 6

Comparison of respiration rate and swimming-speed relationships in menhaden (25.5–26 cm FL, 283–327 g wet wt) (Table 1, our study) and sockeye salmon, *Oncorhynchus nerka* (18 cm TL, 50 g wet wt) (Brett, 1964).

to routine rates calculated from Hettler's data (Table 3) that indicate that a 300-g menhaden at 10°C would have a routine metabolic rate of 0.073 mg O_2/(g wet wt · h) and to previously cited observations by Durbin et al. (1981) on routine swimming and metabolic rates in menhaden at 20°C. Johnstone et al. (1993) reported routine metabolic rates of 0.118 mg O_2/(g wet wt · h) for 290–380 mm Atlantic mackerel, *Scomber scombrus*, swimming at 0.6 BL/s at 11.1°C, and 0.093 mg O_2/(g wet wt · h) for 255–310 mm Atlantic herring, *Clupea harengus*, swimming at 0.3 BL/s at 9.3°C. Because these routine swimming speeds were lower than previously reported by these investigators (0.9–1.2 BL/s for mackerel, and 2 BL/s for herring) and because the fish were maintained for a prolonged period in the respirometer without feeding (5–16 d for mackerel, 13 d for herring), these may be under-estimates. Routine activity and metabolic rates in menhaden thus may be lower than in herring and mackerel.

Durbin et al. (1981) noted that the actual measured routine metabolic rate in menhaden was higher than that predicted for the same swimming speed by using the swimming-speed and metabolic-rate relationship during feeding. This higher routine rate was assumed to reflect increased excitability in fish when not occupied by feeding and also the more variable and energetically less efficient mode of swimming associated with routine activity. Routine swimming also appears to be energetically more expensive than forced swimming (as shown in our study) and directed swimming, where the optomotor response is used to induce fish to swim at a steady, but possibly more variable, speed than in forced swimming. In a review of ten species, three marine and seven freshwater, Boisclair and Tang (1993) found that routine swimming was energetically the most expensive and, on average, was 9.4 times higher (range: 6.4 to 14.0) than forced swimming at the same speed. Directed swimming ranged from 1.0 to 2.8 times as expensive. Applying a similar analysis to menhaden at

Table 3

Comparison of Q_{10} for standard (R_{Std}) and routine (R_{rout}) metabolism in Atlantic menhaden, *Brevoortia tyrannus* (this study and Hettler, 1976, respectively), with standard metabolism in sockeye salmon, *Oncorhynchus nerka* (Table II in Brett, 1964). Hettler's data were extrapolated to a 300-g menhaden by using regressions in his Table I.

	Menhaden (this study)		Menhaden (Hettler, 1976)		Sockeye (Brett, 1964)			Menhaden (this study)	Menhaden (Hettler, 1976)	Sockeye (Brett, 1964)
Temp °C	Wt (g)	R_{Std} (mg O_2/(g · h))	Wt (g)	R_{Rout} (mg O_2/(g · h))	Wt °C	R_{Std} (mg O_2/(g · h))	Temp °C	Q_{10}	Q_{10}	Q_{10}
5					50	0.041				
10	327	0.040	300	0.073	50	0.060	5–10			2.2
15	303	0.073	300	0.127	50	0.071	10–15	3.3	3.0	1.4
20	283	0.087	300	0.149	50	0.120	15–20	1.4	1.4	2.9
24					50	0.195	20–24			3.4
25			300	0.231			20–25		2.4	
							5–24			2.2
							10–20	2.2	2.0	
							10–25		2.1	

20°C, we first calculated from Table 1 the metabolic rate for forced swimming at the routine speed (12.2 cm/s) = 0.111 mg O_2/(g wet wt · h) and subtracted the standard metabolic rate from Table 3 (0.087 mg O_2/ (g wet w · h) to obtain the net cost of swimming = 0.024 mg O_2/(g wet wt · h). The net cost of routine swimming (Durbin et al., 1981) is 0.1 – 0.087 = 0.013 mg O_2/(g wet wt · h). The ratio of the two (= swimming cost ratio [SCR] of Boisclair and Tang, 1993) = 0.024/ 0.013 = 1.8. This value is much lower than Boisclair and Tang's (1993) average SCR value of 9.4 for the ratio of routine to forced swimming costs and is more comparable to their average SCR value of 1.6 for the ratio of directed to forced swimming costs. This suggests that routine activity in menhaden, although energetically more expensive than sustained swimming, is relatively economical. Metabolism associated with routine activity is, in fact, only slightly elevated above standard metabolism in menhaden. Menhaden thus may be an exception to the rule (Webb, 1991) which states that routine metabolic rates of swimming menhaden are not quasi-steady but are substantially higher than forced-swimming rates.

The cost of swimming in menhaden increases exponentially with a linear increase in swimming speed (Fig. 5, this study; Durbin et al., 1981), a pattern characteristic of fish in general (reviewed by Brett and Groves, 1979). The relation between the metabolic cost of swimming and temperature is similar for unfed Atlantic menhaden and sockeye salmon (*Oncorhynchus nerka*) (Fig. 6; Table 2). In both species, the rate of increase in respiration rate per increment of swimming speed is highest at the lowest temperature. With increasing temperature the slopes of the relationships decrease, indicating that the metabolic cost of swimming declines. The cost of swimming to unfed Atlantic menhaden is close to Beamish's (1978) mean value for eight species, where metabolism increased by 2.3-fold for a 1 BL/s increase in swimming speed. Thus we conclude that the metabolic cost of swimming in nonfeeding menhaden is similar to that of other pelagic fish species.

Conversely, the cost of swimming to menhaden while filter-feeding is much higher, where the metabolic rate rose five-fold per BL/s increase in swimming speed (Eq. 2 in Table 2, Durbin et al., 1981), compared with a 1.65-fold increase in unfed fish at 20°C (Table 2, our study). Durbin et al. (1981) speculated that the very high cost of swimming during filter feeding was related to the increased hydrodynamic drag of the expanded gill opercula and the long gill rakers that strain plankton from the water. Present results permit the separation of metabolic rate during feeding into its component parts at 20°C (Table 4; Fig. 7). We observed that during filter feeding, menhaden swam at a preferred speed of about 41.3 cm/s over a wide range of plankton concentrations. However, after prey concentrations had been reduced to subthreshold levels, feeding ceased and activity and respiration both returned to routine levels where there was no postfeeding respiration peak (Durbin et al., 1981). Standard metabolism accounted for only 18.1% of the total metabolism, and the energy demand for swimming was about 22.9%. The remaining 59% of metabolism was associated with the energy cost of feeding, which includes the increased drag of the filtration apparatus, and the metabolic cost of processing the food (specific dynamic action [SDA]). SDA could not be distinguished from total metabolism during feeding (Durbin et al., 1981) because food is processed very rapidly as was shown by the fact that 50% of nitrogen was excreted 1.4 h after ingestion (Durbin and Durbin, 1981) and by the lack of a postfeeding respiration peak. The high cost of filter feeding in the menhaden provides an interesting contrast with a sedentary, ambush predator such as the Northern pike, where the energy required for prey capture is relatively small and where most of the cost of feeding is associated with SDA during an extended postfeeding period of digestion (Lucas et al., 1991).

Table 4

Partitioning of metabolism during filter feeding in Atlantic menhaden *Brevoortia tyrannus*, swimming at their preferred speed of 41.3 cm/s at 20°C. Components of the energy budget: total metabolism during feeding (R_{Feed}); total metabolism nonfeeding but swimming at the same speed ($R_{Nonfeed}$); standard metabolism (R_{Std}); metabolism associated with swimming (R_{Swim}); metabolism associated with filter feeding (R_{Filter}); metabolism associated with digestion and transformation of the food (R_{SDA}). R_{Feed} from Durbin et al. (1981); remaining data from this study.

Metabolic budget		mg O$_2$/(g wet wt · h)	Percent of total
R_{Feed}	$= R_{Std} + R_{Swim} + R_{Filter} + R_{SDA}$	0.480	100
$R_{Nonfeed}$	$= R_{Std} + R_{Swim}$	0.197	
R_{Std}		0.087	18.1
R_{Swim}	$= R_{Nonfeed} - R_{Std}$	0.110	22.9
$R_{Filter} + R_{SDA}$	$= R_{Feed} - R_{Std} - R_{Swim}$	0.283	59.0

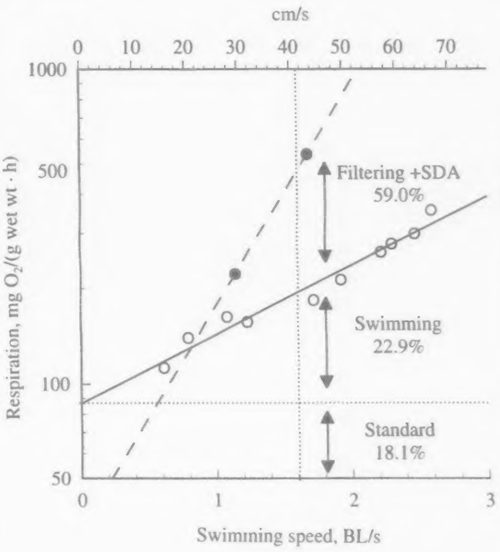

Figure 7

The energy budget of Atlantic menhaden during foraging at the preferred swimming speed, 41.3 cm/s (Durbin et al., 1981) partitioned by the vertical dotted line into the energy required for standard metabolism (horizontal dotted line), swimming (solid line), and feeding (dashed line) = filtering + SDA.

The bioenergetics of feeding differ between filter feeders, such as menhaden, and particulate feeders that consume zooplankton by individual capture. Prey consumption increases linearly with prey concentration and predator swimming speed for filter feeders but increases hyperbolically (Durbin, 1979) for particulate feeders because of the limitations of handling time. The energy cost is higher for filter feeding than for particulate feeding. Both feeding modes are energetically more expensive than routine swimming (James and Probyn, 1989). The optimal swimming patterns in relation to food concentration and foraging time therefore differ between filter and particulate feeders (Ware, 1975; Durbin and Durbin, 1983). Many planktivorous fishes switch between filter and particulate feeding, according to the size and concentration of prey in the water (northern anchovy: Leong and O'Connell, 1969; O'Connell, 1972; Hunter and Dorr, 1982; cape anchovy: James and Probyn, 1989; pilchard: van der Lingen, 1994; Pacific mackerel: O'Connell and Zweifel, 1972; Atlantic herring: Gibson and Ezzi, 1985, 1990, 1992). The switch between filter and particulate feeding can be predicted from the relationship between energy gain and expenditure as the plankton size spectrum changes (Crowder, 1985; James et al., 1989; Gibson and Ezzi, 1992). In contrast, Atlantic menhaden are less flexible in their feeding behavior and consequently may be restricted to coastal and estuarine waters of high production because energetic costs of filter feeding are high and because a relatively small volume of water is searched with mode of feeding (Durbin and Durbin, 1983).

However, menhaden flourish in their chosen habitat, and as omnivores specializing in the smaller size spectrum of particulate material, they have no important competitors among the fishes. Herring and mackerel eat larger zooplankton and live further offshore. The small anchovies that live in the menhaden's range are exclusively zooplanktivores (Bigelow and Schroeder, 1953). Mesozooplankton are competitors for both food and prey of the menhaden (Peck, 1893; Durbin and Durbin, 1975). Menhaden are important in nearshore food webs as primary herbivores and are a major prey species for predatory fishes (Bigelow and Schroeder, 1953; Friedland et al., 1989; Baird and Ulanowicz, 1989); because of their great abundance, they support one of the largest domestic finfisheries in the United States (Ahrenholz et al., 1987).

Acknowledgments

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The relation between otolith size and larval size at hatching for Atlantic cod, *Gadus morhua**

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Abstract.—We examined the relationship between otolith size and larval standard length (SL) at hatching for Atlantic cod, *Gadus morhua*, on the Scotian Shelf. We found a weak correlation between SL and area-based and radius-based measures of size of both lapillar and sagittal otoliths. Correlations of SL with the area of the lapillus were strongest. However, the predictive ability of all relationships was low. For example, the range of predicted SL at hatching of larvae with lapilli of average area included more than 90% of observed SLs in newly hatched larvae from the Scotian Shelf collected over two spawning seasons. These results suggest that otolith-based attempts to backcalculate the size of cod larvae may be prone to substantial error if sizes of particularly young larvae are estimated. We recommend that, where possible, stock- and season-specific estimates of the relationship between the area of the lapillus and larval size at hatching be used in back-calculation techniques.

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The variation in year-class strength in fish populations has profound implications for our ability to manage stocks wisely. Recently, considerable effort has been focused on trying to understand why the few individuals that survive do so, rather than why the majority die (Crowder et al., 1992). This approach, which relies inherently on characterizing traits in individual fish, has been widely applied in both marine and freshwater studies (Herman et al., 1996; Rice et al., 1997 for example). The philosophy behind the approach is that by understanding how survivors differ from those that die, one may expose the mechanisms that regulate recruitment (Fritz et al., 1990).

We used this approach to explore recruitment mechanisms in Atlantic cod, *Gadus morhua*, on the Scotian Shelf. In this area, cod spawning is bimodal, beginning in late October and continuing to the following April, with peaks in December and March (Miller et al., 1995). Recent studies have suggested the importance of small-scale physical oceanographic features, such as gyres and fronts, for larval survival (Taggart et al., 1996; Lochmann et al., 1997). Abundant populations of copepods, particularly *Pseudocalanus* and *Paracalanus*, co-occur with cod larvae (McLaren and Avendaño, 1995) and support rapid larval growth. By following birth-date cohorts through time and repeatedly estimating the distribution of phenotypic and genotypic traits in the cohort, we hoped to quantify whether survivors were different functionally from the majority that died, or whether they were simply lucky (Miller, 1997).

Genetic evidence suggests that cod larvae collected on the Scotian Shelf originate from distinct spawning events (Ruzzante et al., 1996). However, Ruzzante et al. (1996) have shown that the genetic structure within the population remains stable over time. Meekan and Fortier (1996) repeatedly sampled two autumn-spawned cohorts of Scotian Shelf cod, following each for approximately six months. The pattern of survival for the two cohorts differed. In 1991–92, the growth rate distribution of survivors differed little from the growth distribution of the cohort from which they were drawn. In contrast, in 1992–93, Meekan and Fortier (1996) found evidence of strong selection for faster growing fish. Moreover, after comparing otolith sizes at hatching, Meekan and Fortier (1996) suggested that the potential for faster growth expressed by the survivors may have been present at hatching.

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Our ability to detect examples of phenotypic selection evidenced above depends on our ability to quantify the distribution of traits in the entire cohort and to hindcast the distribution of traits in the survivors (Miller, 1997). For much of the research discussed above, and for many other individual-based studies, otolith microstructural analysis is used to detect phenotypic selection. However, to apply this approach, three requirements must be satisfied (Francis, 1990): 1) primary increments must be deposited at a known and consistent rate; 2) there must be a quantifiable relationship between growth and the width of increment rings; and 3) the initial otolith size, defined by the presence of a check mark, must be related to the size of the fish at the formation of the check.

For cod, the regularity of increment deposition has been verified and validated (Bergstad, 1984; Radtke, 1984; and see Geffen, 1995, for a recent example). Thus, the first condition for back calculation has been satisfied in cod. However, there remains considerable uncertainty over the status of the remaining two conditions. The relationship between somatic and otolith growth in cod is unclear (see Geffen, 1995, and Meekan, 1997, for opposing views). The lack of a clear relationship between rates of somatic and otolith growth may result from the natural variability among and within many cod populations (Brander, 1994; Chambers, 1997). Typcially, cod larvae grow at highly variable rates, and somatic and otolith growth may become disassociated (Suthers et al., 1989; Campana and Hurley, 1989; Geffen, 1995). Concerns over the validity of the assumed relationship between fish and otolith size at hatching also arises because of inter- and intrapopulation variation. Considerable variation has been reported in larval size at hatching both within and among populations (Bolz and Lough, 1983; Bergstad, 1984; Radtke, 1984; Knutsen and Tilseth, 1985; Miller et al., 1995). Currently, no clear link between otolith size and larval size at hatching has been established for any population.

The objective of this paper is to examine the relationship between otolith size at hatching and larval size at hatching for cod. Specifically, we address whether otolith size at hatching is significantly correlated with larval size at hatching, and whether all otoliths provide an equally accurate and precise estimate of larval size at hatching. We use data collected for cod on the Scotian shelf collected between 1991–93 to address these questions.

Methods

Sampling was carried out during 29 cruises on the Scotian Shelf between March 1991 and May 1993 (Fig. 1). O'Boyle et al. (1984) have given a general description of the Scotian Shelf system. Full details of the sampling method are given by Miller et al. (1995). We summarize the general sampling design here and provide additional details that relate to the specific objectives of this study.

Twenty six cruises were designed to provide broad-scale information on temporal and spatial distributions and abundance of cod eggs, larvae, and juveniles (Fig. 1). We sampled a rectangular grid of 45

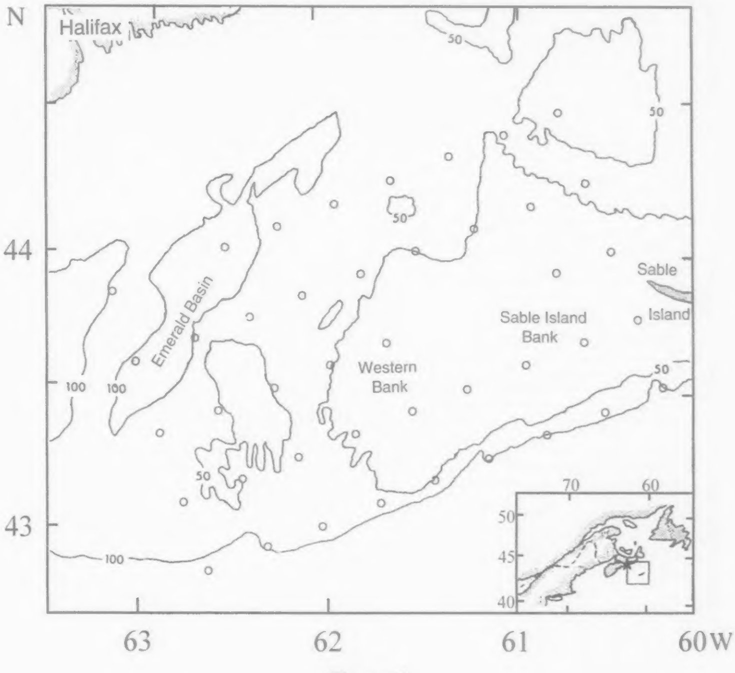

Figure 1

Map of Scotian Shelf showing the area of sampling locations. Shown on the figure are the 50- and 100-m depth contours, the principal sampling locations within the 45-station grid (open circles), and the location of Halifax, NS, Canada, for reference.

stations at roughly monthly intervals using either paired 0.61-m bongo nets fitted with 333-µm mesh nets, an 8 + 2 m rectangular mid-water trawl (RMT) fitted with 1600-µm and 333-µm mesh nets, or a paired 1.4 m^2 rectangular frame net, fitted with 333-µm mesh nets. Depth information for both the bongo and frame net was estimated from cable angles and lengths deployed. The RMT was fully equipped and provided continuous, real time depth, temperature, salinity, and volume filtered data. The station exhibiting the highest concentration of cod larvae was resampled with a BIONESS sampler equipped with ten 1-m^2, 333-µm mesh nets, that was deployed to sample discrete 5-m depth strata in the upper 25 m of the water column and 10-m depth strata at deeper depths. Three of the 29 cruises were designed to track a patch of eggs and larvae over smaller spatial scales for up to 20 days in order to track how traits changed over time. On these cruises we deployed principally a BIONESS sampler and bongo nets. However, because we were attempting to sample continuously from the same patch of water, stations were distributed irregularly in space.

All net samples were sorted and cod eggs were removed on board ship. Late-stage eggs that appeared healthy and undamaged by the collection process were videotaped under a dissecting microscope at 6–50× magnification. Individual eggs were incubated separately on a 12-h light:12-h dark cycle and at near-ambient temperature. Light from blue incandescent bulbs mimicked the light environment at depth. Nursery temperatures were recorded daily. All eggs from the same cruise were incubated at the same temperature. However, because sea temperatures varied across the sampling grid, and with depth, there were unavoidable differences between incubation and ambient temperatures for individual eggs. Vials were checked every 12 hours for hatching. When a larva hatched, it was immediately videotaped and stored in liquid nitrogen prior to otolith extraction and analysis.

In the laboratory, lapillar and sagittal otoliths were removed from larvae and mounted in cyanoacrylic cement. In most larvae we could remove and classify successfully all four otoliths. Otoliths were examined under bright field illumination under a compound microscope at 60–1000× magnification. Oil immersion was required for the higher magnifications.

Videotape recordings and otolith images were analyzed in the laboratory by using an image analysis system (Optimas v3.11, Bioscan Corporation, Seattle WA). We staged each egg according to Thompson and Riley's (1981) system. Egg diameters were calculated from three digitized points on the circumferences of eggs. From these points the diameter was calculated as

$$Diameter = \frac{abc}{4\sqrt{s(s-a)(s-b)(s-c)}},$$

where a, b, and c = the lengths of the chords connecting the three points; and
s = $2(a + b + c)$.

Larvae that hatched from these eggs were measured to standard length (SL). Only undamaged otoliths were analyzed. Several measures were taken to describe otolith size. At this early stage, otoliths were essentially spherical in cross section. We measured the cross-sectioned area of both lapillar and sagittal otoliths. We also measured the radius of the otolith at hatching because this is the most common measurement used when estimating larval hatching sizes from otolith data.

Analysis of the data collected depended upon the purpose to which the analysis was being put. For univariate analyses to determine seasonal trends in a trait, data were aggregated to provide a mean value for each deployment before analysis. This approach reflects the sampling design employed in the field, and thus the deployment is the appropriate sampling unit. However, for bivariate analyses to determine the correlation among measures of otolith size and between otolith size and fish size, the individual fish is the appropriate sampling unit, and thus these analyses were conducted at the individual level.

Results

We identified and incubated 650 cod eggs from April 1991 to May 1993. Of this total, 259 (39.9%) successfully hatched. Otoliths from a random sample of 73 of these larvae were used in our analyses. We obtained reliable measurements from both lapilli on 56 larvae (76.7%) and from both sagittae for 59 (80.1%) larvae. The distribution of data, by month and year, is given in Table 1.

We examined the correlation structure in the data for area of otolith and radius of otolith at hatching. Estimates of otolith area were correlated among otolith types, but there were no significant correlations among otoliths from the same side of the body (Fig. 2). Moreover, the correlation among lapilli was greater than that for sagittae (Fig. 2). An identical pattern was found with respect to radius of otolith at hatching (Fig. 3).

We regressed each measure of otolith size on larval size at hatching, using only otoliths from the left side of the body. The area of the lapillus (LA) and SL at hatching were significantly and positively related (Fig 4A). Overall, longer larvae have bigger lapilli. The 95% CIs around the predicted mean were nar-

Table 1

Mean size (±SD) and number of newly hatched cod larvae from the Scotian Shelf providing data for otolith analysis by month and year. Otolith mean and SDs are calculated by using estimates for both otoliths of the specified type within each fish. Shown for each entry are the mean (upper number), SD (middle number in parentheses), and number of fish providing data for analyses (lower number).

	1991–92				1992–93			
Measurement	Nov	Dec	Jan	Mar	Oct	Dec	Mar	Total
Egg diameter (mm)	1.35 (0.1) 43	1.45 (0.07) 37	1.35 (0.05) 11	1.51 (0.1) 2	1.38 (0.06) 91	1.51 (0.06) 40	1.59 (0.09) 35	1.47 (0.1) 259
SL at hatching (mm)	4.31 (0.2) 43	4.43 (0.3) 37	5.04 (0.2) 11	5.34 (0.3) 2	4.03 (0.3) 91	4.52 (0.3) 40	5.03 (0.3) 35	4.38 (0.5) 259
Lapillar area (μm^2)	493.0 (113.9) 6	529.5 (66.1) 7	696.49 (98.5) 5	732 1	360.69 (74.0) 10	562.51 (113.2) 8	584.48 (90.5) 19	537.34 (131.6) 56
Lapillar radius at hatching (μm)	13.6 (1.4) 6	14.12 (0.8) 7	15.87 (1.1) 5	15.87 (0.9) 1	11.71 (1.2) 10	14.80 (1.0) 8	14.74 (1.6) 19	14.13 56
Sagittal area (μm^2)	191.3 (69.6) 6	270.29 (83.1) 11	369.12 (108.6) 5	360.57 (50.9) 1	227.25 (84.9) 10	333.37 (64.1) 8	280.71 (85.9) 18	276.6 59
Sagittal radius at hatching (μm)	8.79 (1.29) 6	10.39 (1.4) 11	11.98 (1.7) 5	11.85 (1.2) 1	9.55 (1.5) 10	11.32 (1.3) 8	10.64 (1.5) 19	10.45 60

row. For a lapillus of average area, the predicted mean larval SL at hatching was 4.55 mm. The 95% CIs around this value were 4.4 mm < SL < 4.66 mm, a range of 0.2 mm. However, in our application we were more interested in the 95% CIs of an individual prediction. The range in these values was much wider, 3.66 mm < SL < 5.41 mm., a range of 1.75 mm. We conducted a similar analysis for the radius of the lapillus at hatching (LR, Fig 4B), which was significantly and positively related to SL at hatching. Overall, longer larvae had wide lapilli at hatching. As with the results for the total area of the lapillus, the 95% CIs for larval SL predicted for a lapillus of average radius were narrow. For a lapillus of average radius at hatching (14.15 μm), the associated 95% CIs of the mean were 4.44 < SL < 4.69 mm, a range of 0.25 mm. However, the prediction is less precise for individual back calculations for the associated 95% CIs of the individual prediction were 3.72 < SL < 5.49 mm, a range of 1.77 mm.

We conducted a similar regression analysis for the area and radius of the sagittae and SL at hatching. There were significant linear relationships for both measures of otolith size and SL at hatching (Fig. 5). For an average sagittal area of 276 μm, the predicted SL at hatching was the same as that for the lapillus. The 95% CIs for the population average were 4.38 mm < SL < 4.75, a range of 0.37 mm. The wider confidence intervals for the population mean for the sagittal measurements compared with the lapillar measurements reflected the lower coefficient of determination (r^2) of the regression. Moreover, the 95% CIs of an individual prediction, based upon sagittal area, were also wider than those for lapillus-based predictions (3.48 < SL < 5.64, a range of 2.16 mm). Similar patterns were observed for the regressions for sagittal radius at hatching (Fig. 5B).

We examined the potential for egg size and temperature to increase the predictive power of the relationships. We performed these analyses on data aggregated to the deployment level. Standard length at hatching was positively related to egg size: $SL = 0.656\ (\pm 0.46) + 2.55\ (\pm 0.31) \times$ egg diameter, $n = 128$, $r^2 = 0.345$, $P = 0.0001$. To explore the potential for egg size to explain additional variation in otolith-size and SL-at-hatching models, we regressed the residuals from the relationship of egg diameter to SL on several measures of otolith size. If egg size explains additional variation, independent of SL at hatching, we would expect to see a significant regression statistic. The residuals were significantly related to the area and the radius at hatching of the

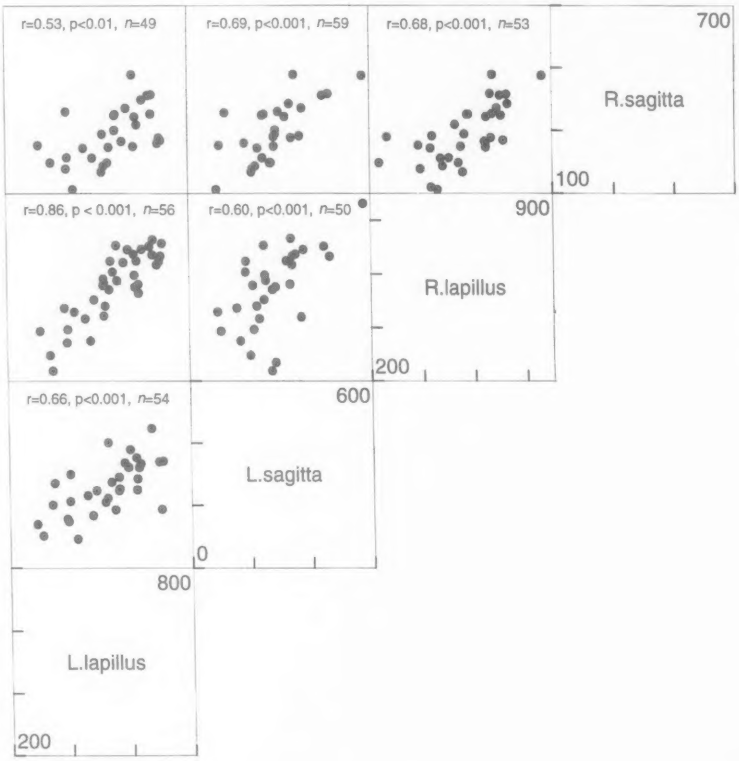

Figure 2

Scatter plots of individual measures of otolith area (μm^2) for newly hatched cod larvae collected on the Scotian Shelf. Correlation coefficients (r) for each relationship are given in each panel.

lapilli (Fig. 6). However, the residuals were not significantly related to either measure for sagittae.

Standard length (SL) at hatching was negatively related to sea temperature at collection: $SL = 5.26 (\pm 0.07) - 0.939(\pm 0.007) \times \text{temp}$, $n = 44$, $r^2 = 0.79$, $P = 0.001$. To explore the potential relationship between otolith size and temperature, we regressed our most predictive estimate of otolith size, lapillar area, against the residuals from the SL-temperature relationship. There was no clear relation between temperature residual and lapillar area (Fig. 7).

Discussion

Otoliths can be used to infer the standard length of cod larvae at hatching. However, our data suggest that the precision with which such inferences can be drawn may not be sufficient to permit accurate comparisons of the size distribution at hatching between survivors and the population at large. On the Scotian Shelf newly hatched cod larvae varied between 2.4 and 6.1 mm SL (Miller et al., 1995). The best regression relationship we developed in our study related SL to area of the lapillus, and explained 35% of the variation in the data. Accordingly, 65% of the variation remained unexplained. The regressions we developed suggest that the 95% confidence intervals of individual back-calculated size at hatching for a fish are wide. Predicted SL for larvae with average-size lapilli ranged from 3.66 to 5.41 mm. This covers fully 48.7% of the total range in initial sizes at hatching observed in cod larvae from the Scotian Shelf. More strikingly, based on estimates of mean and variation of SL given by Miller et al. (1995), this range includes 91% of all newly hatched cod larvae on the Scotian Shelf. Back calculations from lapillar otoliths larger or smaller than average size will be even more imprecise. Thus, we conclude that estimates of initial size in cod larvae are unlikely to be sufficiently pre-

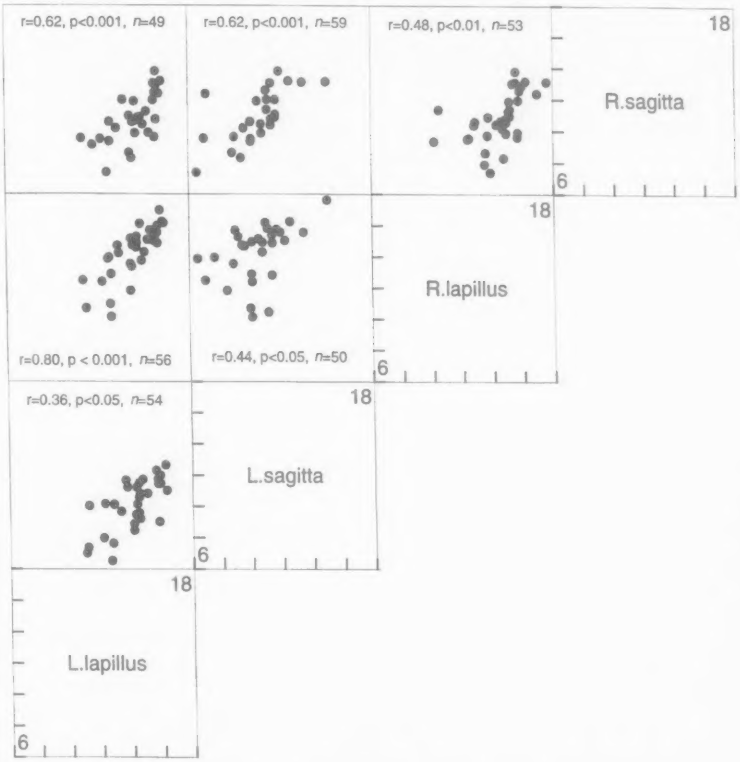

Figure 3

Scatter plots of individual measures of otolith diameter (mm) at hatching for newly hatched cod larvae collected on the Scotian Shelf. Correlation coefficients (r) and significance for each relationship are given in each panel.

cise to detect anything other than substantial differences in hatching size among the survivors and the initial cohort.

Meekan and Fortier (1996) reported evidence that surviving cod larvae on the Scotian Shelf in 1992–93 were significantly different from the cohort from which they originated. In contrast, survivors did not differ from the cohort at large in 1991–92. Meekan and Fortier (1996) suggested that the change in radius at hatching that they observed in 1992–93 was evidence of selection for faster growing larvae in that cohort. Meekan and Fortier's suggestion, as it relates to the relative sizes of otoliths in the survivors and the initial cohort, is indisputable. Our findings that the size of a larva and its otoliths are weakly correlated do not allow us to reject the notion that survivors may have differed in size at hatching from the overall cohort. Our results suggest an additional explanation. We report here a significant relationship between otolith size and the residual from the predicted relationship between egg and larval sizes. Larvae that hatch from relatively larger eggs, which have relatively larger yolks, have larger otoliths. Hence, we agree with the Meekan and Fortier's (1996) suggestion, but we would further hypothesize that the difference observed may have been caused by variation in egg size rather than by variation in larval size at hatching directly. If correct, we suggest that the greater amount of yolk in larger eggs enhanced initial larval growth and survival. An understanding of the actual mechanism responsible for these faster growing larvae will require additional analyses.

Our results suggest that attempts to backcalculate size of cod larvae will be most successful if they are based on measurements from the lapillus. Although larval SL at hatching was significantly related to all measures of otolith size, relationships involving the lapillus explained more variation than corresponding relationships involving the sagitta. Moreover, regressions involving the projected area of the lapil-

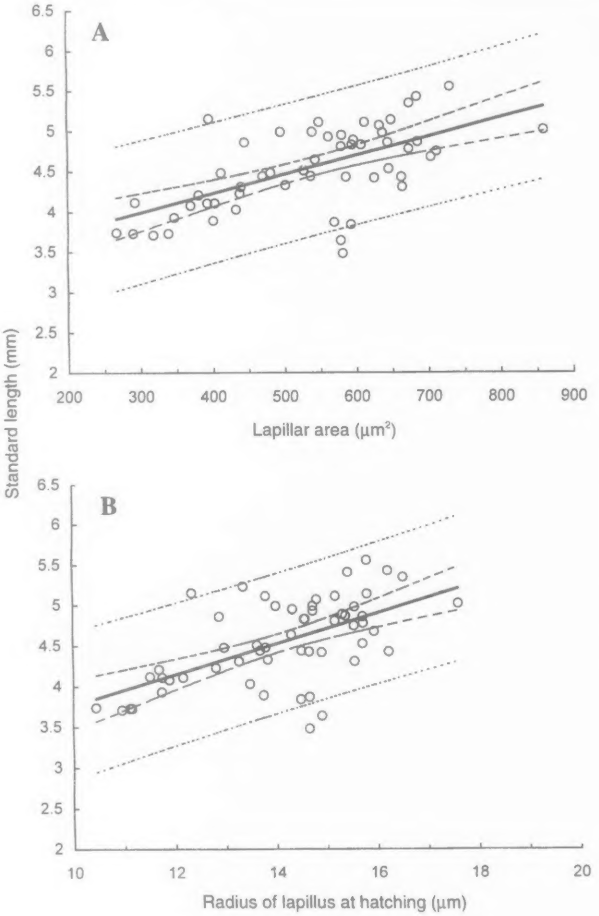

Figure 4

Relation between standard length (SL) at hatching of individual larvae and (**A**) the lapillar area (LA), and (**B**) the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $LA = 3.295\ (\pm 0.24) + 0.0023\ (\pm 0.0004) \times SL$, $n = 54$, $r^2 = 0.35$, $P = 0.0001$; $LR = 1.898\ (\pm 0.51) + 0.188\ (\pm 0.036) \times SL$, $n = 54$, $r^2 = 0.35$, $P = 0.0001$.

lus were more accurate than those involving the radius of the lapillus at hatching. We conclude from these findings that attempts to hindcast size at hatching in cod should rely on measurements taken from the lapillus and, where possible, should use the cross-sectional area of the otolith as the measure of otolith size. It has been recognized that cod lapilli are larger initially than sagittae, but that sagittae increase in size more rapidly (Bergstad, 1984; Radtke, 1984; Campana and Hurley, 1989). Lapilli remain larger than sagittae for up to 25 days. As a result, back calculations involving cod older than 25 d or larger than 6–8 mm have been based on sagittae instead of lapilli. However, the relative sizes of the otoliths at their core remain unaltered by subsequent growth dynamics. Hence, we caution that, even though the sagittae in these larger and older fish are larger absolutely than the lapilli, the precision of estimates of initial size at hatching will be most precise if the estimates are based on the size of the lapillus at hatching.

In controlled laboratory experiments, Geffen (1995) found that the otolith-size and fish-size relationship

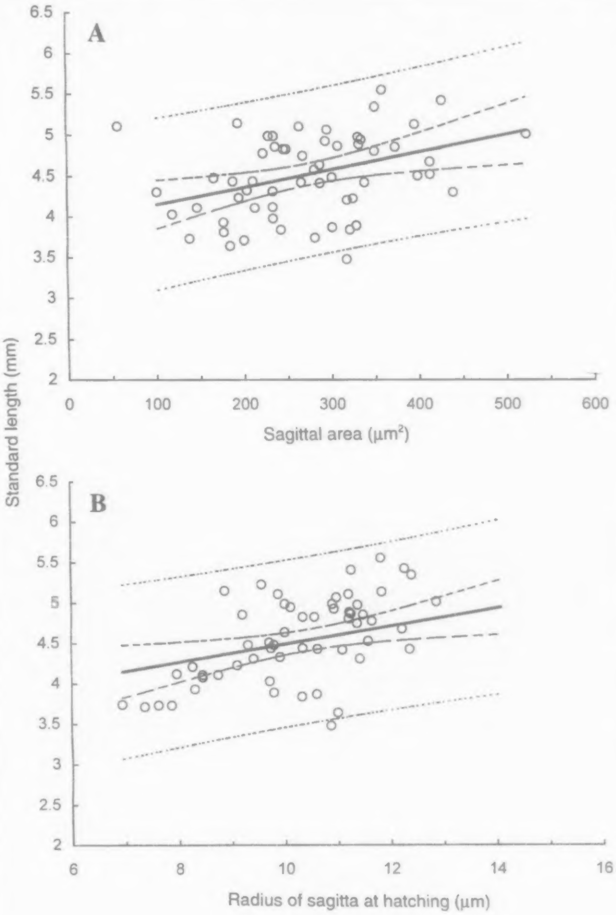

Figure 5

Relation between size at hatching of individual larvae and (**A**) the sagittal area (SA), and (**B**) the sagittal radius (SR) at hatching for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $SA = 4.033\ (\pm 0.21) + 0.00178\ (\pm 0.0007) \times SL$, $n = 58$, $r^2 = 0.09$, $P = 0.017$; $SR = 3.44\ (\pm 0.45) + 0.104\ (\pm 0.043) \times SL$, $n = 59$, $r^2 = 0.09$, $P = 0.018$.

could predict overall mean population growth rates extremely well but that they were unreliable predictors of individual larval growth. For example, Geffen (1995) reported that within 15 d of hatching, otolith growth and a measure of somatic growth were poorly correlated in cod larvae. If Geffen's conclusion reflects a broad pattern, her results have profound implications for any application of an individual-based backcalculation approach to cod. Recently, Meekan (1997) pointed out that Geffen's conclusions may have been affected by experimental conditions and by the use of a single mean value of larval size at hatching as the origin of the relationship between larval size and otolith size. Larval size at hatching varies substantially in cod (Knutsen and Tilseth, 1985; Miller et al., 1995), and thus Geffen's use of a single size at hatching is unrealistic and cannot be supported by the data available. Yet it is not clear what value one should use for the origin in backcalculating growth trajectories.

Our data suggest that the wide variability in the relationship between otolith size and hatching size observed in cod will likely plague attempts to

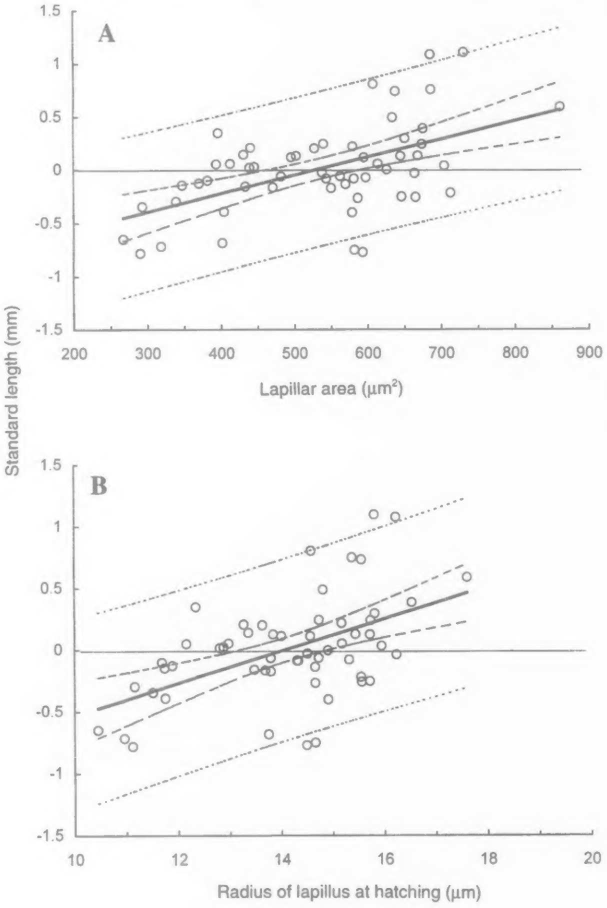

Figure 6

Relation between the residuals from the mean SL and mean egg diameter and **(A)** the lapillar area (LA) and **(B)** the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are: $Residual = 0.00162\ (\pm 0.0003) \times LA - 0.721\ (\pm 0.186)$, $n = 37$, $r^2 = 0.38$, $P = 0.0001$; $Residual = 0.126\ (\pm 0.03) \times LR - 1.633\ (\pm 0.39)$, $n = 37$, $r^2 = 0.37$, $P = 0.0001$.

backcalculate to early periods of the life history. Geffen (1995) commented on the variability in the sizes of hatchmarks on the lapilli of cod larvae. She reported estimates of otolith diameters at hatching that varied by more than twofold (13.7–28.4 μm). In Figure 8, we summarize published data on SL and lapillar diameter at hatching for a range of cod stocks. The variability evident in Figure 8 suggests that the choice of a "biological intercept" for cod is problematical (Campana, 1990); a single "best" size at hatching or otolith size at hatching clearly cannot be defined for cod. However, the data do show that an overall relationship between the mean SL at hatching and the mean diameter of lapillus exists. However, given the limited data set, the relationship is statistically insignificant ($MDL=1.73 \times MSL + 19.54$, $r^2=0.306$, $n=7$, $P>0.05$). With these results, we recommend that extreme caution be exercised when selecting parameter estimates for use in the back calculation of size-at-age in cod.

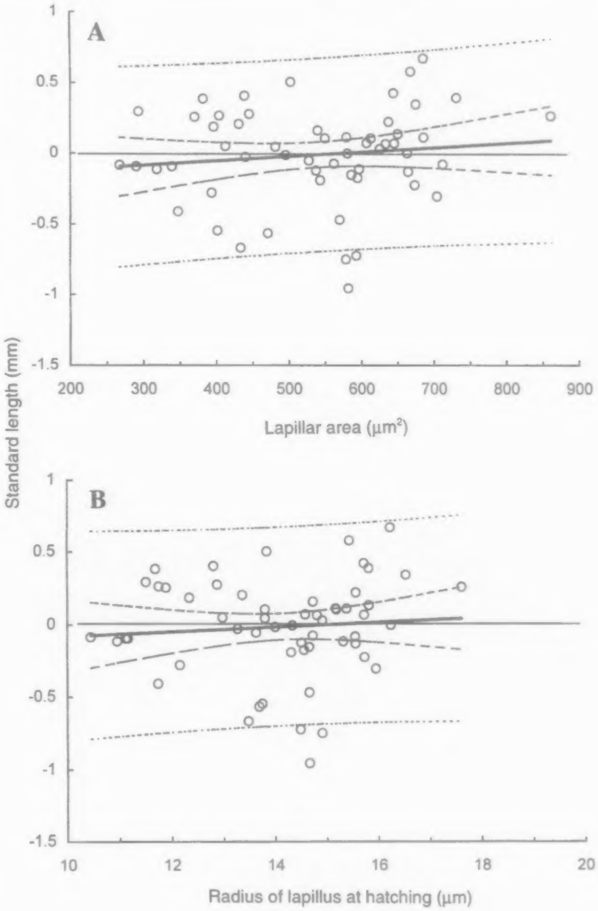

Figure 7

Relation between the residuals from mean SL and mean water temperature at collection and (**A**) the area of the lapillus (LA) and (**B**) the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $Residual = 0.00021\ (\pm 0.00027) \times LA - 0.102\ (\pm\ 0.143)$, $n = 37$, $r^2 = 0.01$, $P = 0.89$; and $Residual = 0.013\ (\pm 0..21) \times LR - 0.184\ (\pm 0.28)$, $n = 37$, $r^2 = 0.001$, $P = 0.85$.

The implications from our results for studies on other species are less clear. It is important to note that one would not expect all species to exhibit the same plasticity in size at hatching, or in the relationship between fish size and otolith size at hatching. Hence, for some species there is little variation in initial size at hatching. In these species the error introduced by assuming a single, universal size at hatching is probably small. However, it is important to recognize that back-calculation techniques all assume a common origin for the family of size-at-age lines that are modeled. The methods differ only in the definition of the origin (fish size at zero otolith size, biological intercept, or otolith size at zero fish size), but all assume a single value. Indeed Campana (1990) noted that relatively little attention had been paid to the effects of variation in the intercept term of back-calculation methods; most attention had been paid to variation in the slope. However, for species that are known to vary widely in hatching size (e.g.

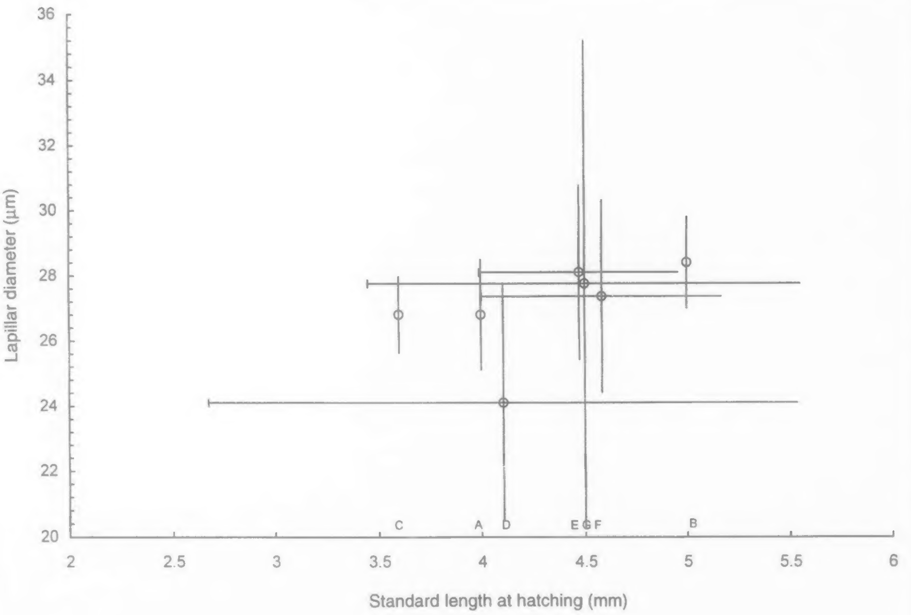

Figure 8

Relation between larval size and otolith size at hatching reported in the literature for different populations of cod. Shown for each data point are means and bivariate standard deviations (when available). The sources for individual data points are shown as letter codes above the abscissa. Codes: (**A**) Radtke (1984); (**B**) Bergstad (1984); (**C**) Radtke (1989); (**D**) Geffen (1995); (**E**) 1991–92 cohort from Meekan and Fortier (1996); (**F**) 1992–93 cohort from Meekan and Fortier (1996); and (**G**) this study. Estimates of SL at hatching for Meekan and Fortier were taken from estimates of mean hatching size for each cohort given by Miller et al. (1995).

Atlantic herring), individual variability in the intercept may be significant. We recommend that, at a minimum, stock specific values for intercepts be used if the interest is in periods of the life history shortly after hatching. Further, caution should be exercised in relating shifts in the back-calculated distribution of radii at hatching to size-selective mortality. More careful study of the relationship between otolith size and fish size in individual species is likely warranted if researchers wish to employ otolith-based back calculation (Chambers and Miller, 1995).

Acknowledgments

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Abstract.–Daily growth increments on otoliths were used to estimate the age of larval and juvenile haddock, *Melanogrammus aeglefinus*, and pollock, *Pollachius virens*, collected on Emerald and Sable Island Banks, eastern Canada, between March 1991 and May 1993. The daily periodicity of the increments was validated from observations of reared larvae. For both species, the first increment was deposited the day after hatching and thereafter one increment was added daily. A Laird-Gompertz growth curve was fitted to length–age data for each species. Growth rates in haddock and pollock larvae varied significantly in different years. For haddock, the lowest growth rate was for the 1993 cohort, and growth rates in 1991 and 1992 cohorts were similar. For pollock, the 1993 cohort had the highest growth rate. The average growth rate was 0.21 mm/d for the first month and 0.42 mm/d for the second month for larval haddock and 0.18 mm/d for the first month and 0.23 mm/d for the second month for larval pollock. Growth continued exponentially after the transition from a primarily pelagic life to a predominantly demersal one, which occurred at an age of about 40–50 d. No indication of a cessation in growth was observed. Analysis of length–age data indicated that the accelerated growth of juveniles after 50 d in age could have reflected the exploitation of a more abundant food resource after settlement. Thus, pelagic and early demersal growth appear to represent distinct stanzas in the growth history of these gadoids.

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Age validation and growth of larval and juvenile haddock, *Melanogrammus aeglefinus*, and pollock, *Pollachius virens*, on the Scotian Shelf

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A central problem in fisheries research is understanding mechanisms determining year-class strength. Growth, which is considered critical to the survival and subsequent recruitment of larval marine fishes (Houde, 1987), is likely strongly affected by temperature and food availability (Ricker, 1979). Food limitation can affect survival directly by causing starvation (Lasker, 1975) or indirectly by retarding growth rate which in turn increases mortality from predators (Rothschild and Rooth, 1982). In addition, feeding conditions may change markedly owing to density independent factors, such as temperature, which can directly affect growth rates (Laurence, 1978).

Ware (1975) suggested that growth and mortality rates interact to determine survival of fish populations. A prediction of this hypothesis is that predation is a major factor affecting year-class strength and that mortality due to predation is inversely related to growth rate (Ware, 1975; Shepherd and Cushing, 1980). This hypothesis assumes that average growth is below the maximum and that feeding conditions that maximize growth are associated with minimal mortality.

Calculation of reliable rates of growth and mortality of larval fish, and determination of when loss due to recruitment is greatest, requires accurate determinations of age. Accuracy and precision of growth estimates for larval fishes have been greatly enhanced by the discovery of daily growth increments on otoliths (Pannella, 1971; reviewed by Campana and Neilson, 1985). Ageing by counting otolith growth increments, along with measurements of the width of the increments, provides a means of estimating the relation between length at age. In this way, growth curves, and even individual growth rates, have been calculated for a variety of species (Brothers et al., 1976; Struhsaker and Uchiyama, 1976; Taubert and Coble, 1977; Radtke and Waiwood, 1980).

Daily increments have been shown to occur in most species, nevertheless validation of the frequency of increment deposition is required before larval age can be estimated from otolith measurements. To validate increment deposition, Geffen (1987) recommended sampling reared larvae throughout the larval stage. This approach had previously been used for a number of species, for example, to determine when the first increment is deposited in Atlantic cod (*Gadus morhua*) larvae (Radtke and Waiwood, 1980) and to validate the daily increment formation in Pacific herring (*Clupea pallasi*) (Moksness and Wespestad, 1989). In the present study, I validated whether increments are deposited daily in haddock otoliths (*Melanogrammus aeglefinus*) using the same approach. Preliminary results on larval pollock (*Pollachius virens*) are also presented. Finally, daily increment analyses are used to estimate age and growth rates of larval and juvenile haddock (*M. aeglefinus*) and pollock (*P. virens*) from the Emerald and Sable Island Banks on the Scotian Shelf off eastern Canada.

Materials and methods

Study area and collection of larvae

The Scotian Shelf is a 62,000 km^2 area with an average depth of 90 m. It is bounded on the southwest by Northeast Channel entering the Gulf of Maine and on the northeast by the Laurentian Channel and Gulf of St. Lawrence. Several shallow offshore banks along the outer edge of the shelf are separated from one another by deeper channels that open onto interior basins having depths of >100 m (O'Boyle et al., 1984). The general water circulation on the Scotian Shelf is dominated by the Scotian current which flows southwesterly and parallel to the Nova Scotia coast and which carries a mixture of slope water and diluted waters from the Gulf of St. Lawrence (e.g. Sutcliffe et al., 1976; Drinkwater et al., 1979).

Eggs, larvae, and juveniles of *M. aeglefinus* and *P. virens* were collected during 20 surveys made on Emerald and Sable Island Banks (Fig. 1) from March 1991 to May 1993 (Table 1), as part of the program of Ocean Production Enhancement Network (OPEN) (Griffin and Anderson, 1993). Sampling was conducted using a grid of 45 stations (Fig. 1) with an interstation spacing of approximately 30 km. A 50-cm bongo frame with 150- and 250-µm mesh nets (March–May 1991) as well as a rectangular midwater trawl (RMT, 2–8 m^2) (Baker et al., 1973) with nets of 2 m^2 (333-µm mesh) and 8 m^2 (1600-µm mesh) were used. At each station, duplicate oblique hauls were made from near the bottom to the surface at 2.0–2.5 knots, with a retrieval time of 30 min. After the standard grid stations were sampled, the area of maximum abundance of larval fish was revisited so that 48 h of vertical sampling could be conducted with a BIONESS sampler (1 m^2) (Eastern Marine Services E-Z-Net, Dartmouth, NS) fitted with ten 333-µm mesh nets (June 1991 to May 1993). Ten discrete depths were sampled every 4 h. Deployment sampling depths were spaced at 5-m intervals, from the bottom to the surface, and fished for 5 min at 2.0–2.5 knots. Most larval haddock and pollock were sorted at sea and preserved in 95% ethanol. Temperature and salinity profiles were recorded at each station with a Sea Bird CTD probe (Sea-Bird Electronics, Inc. Bellevue, WA) connected to the electronics unit of the RMT or BIONESS sampler, or both. When the RMT or BIONESS, or both, were not used, independent CTD casts were made at each station.

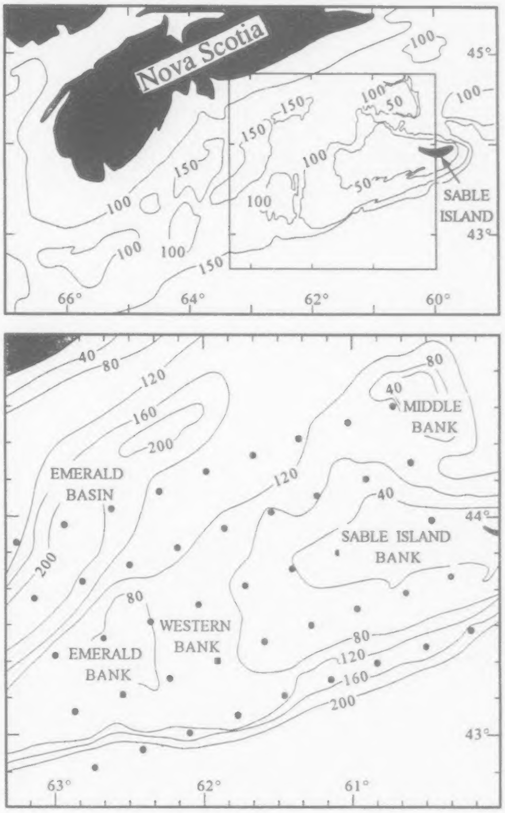

Figure 1

Study area showing stations where larval and juvenile haddock and pollock were collected on the Scotian Shelf from March 1991 to May 1993. Isobaths are in meters.

A subset of pollock and haddock larvae were videotaped at sea by using a stereo dissecting microscope connected to a video camera and a magnetoscope and were then individually preserved in 95% ethanol. One to two months later, each fish was measured in the laboratory to the nearest 0.1 mm with a stereo dissecting microscope with an ocular micrometer. The unpreserved standard lengths were measured from video images recorded at sea and projected on a television monitor linked to an image analysis system. Linear regression of unpreserved standard length (SL, obtained from the videotape) to preserved standard length (*PSL*, after preservation in ethanol) for haddock ($SL=1.531 + 1.005PSL$, $n=129$, $r^2=0.99$) and pollock ($SL=0.710 + 0.969PSL$,

Table 1

Station information for larval and juvenile of haddock and pollock collected for otolith analysis from March 1991 to May 1993 on the Scotian Shelf. Values in parentheses are total larvae sampled.

				No. of larvae examined		Mean SL of larvae (mm)		Mean no. of increments	
Cruise	Vessel	Date	T (°C) at 30 m	Haddock	Pollock	Haddock	Pollock	Haddock	Pollock
91–01	*Petrel V*	5–11 Mar	4.0	0 (3)		3.9		—	
91–02	*Petrel V*	16–24 Apr	5.0	2 (97)		4.6		14	
91–04	*Petrel V*	17–26 May	7.0	1 (22)		7.6		23	
91–99	*Cape Keltic*	17–22 Jun	8.3	93 (164)		20.2		60	
91–08	*Petrel V*	18–27 Jul	13.5	18 (18)		60.8		105	
91–16	*Petrel V*	12–21 Nov	8.8		4 (16)		3.9		4
91–17	*Petrel V*	7–16 Dec	7.3		12 (23)		5.1		9
92–18	*Petrel V*	7–18 Jan	5.2		88 (98)		5.7		11
92–19	*Petrel V*	16–26 Feb	2.3	0 (9)	80 (218)	5.1	10.7		29
92–20	*Petrel V*	10–20 Mar	1.6	12 (66)	17 (61)	4.9	12	2	41
92–21	*Petrel V*	5–14 Apr	2.0	9 (40)	7 (33)	4.7	15	3	44
92–23	*Petrel V*	17–26 May	3.8	65 (328)	2(2)	8.1	22	21	70
92–98	*Cape Keltic*	17–22 Jun	7.3	16 (47)		22		60	
92–26	*Petrel V*	21–25 Jul	13.7	5 (5)		31.1		66	
93–32	*Petrel V*	11–22 Jan	4.0		246 (1005)		5.4		5
93–33	*Petrel V*	15–25 Feb	2.1		54 (57)		9.9		27
93–34	*Petrel V*	19–26 Mar	1.7	138 (266)	5 (5)	4.4	15.1	4	54
93–35	*Petrel V*	16–24 Apr	3.7	116 (239)	4 (4)	7.2	13.5	16	48
93–37	*Petrel V*	16–24 May	5.6	127 (290)	0 (10)	12.4	15.5	33	

n=8, r^2=0.99) were used to calculate the unpreserved standard length (SL) of fish preserved in ethanol.

Validation of ageing technique

To determine if the increments observed in otoliths of haddock and pollock were deposited daily, fertilized eggs collected in a 333 µm mesh net from the RMT were reared on the ship. Haddock eggs were collected at the Western and Emerald Banks area, February–April 1992 and 1993. Spawning begins in February around the Western Bank. Eggs were taken in the same general area on any given sampling date from February to April in both 1992 and 1993.

Some pollock eggs were collected in January–February and April 1992, as well as in October–November 1992 and January and March 1993. At the beginning of the spawning season, eggs were detected at the southeast of Sable Island Bank. In January–February the eggs were collected on the Western Bank, and in March–April the distribution of eggs included Emerald Bank. The spawning of pollock and haddock overlapped during February–April because the eggs of the two species were found together.

Immediately after the nets were brought aboard the vessel, the most advanced stages of eggs were sorted and individually placed in 20-mm vials filled with seawater which had been passed through 1-µm Hytrex filters. At this time it was impossible to distinguish between the eggs of the two species (Brander and Hurley, 1992). They were reared at 4°C in a conventional refrigerator on the ship. The photoperiod was kept at 12:12 h with dim blue light. As each egg was monitored twice daily to establish when hatching occurred, the maximum error in hatching time determinations was 12 h. After hatching, 136 zero to eleven-day haddock larvae, and nine zero to four-day pollock larvae were killed and preserved in 95% ethanol. Twelve additional 0–2 d old haddock larvae (collected on April 1993) were obtained from Flodevigen Marine Research Station, in Arendal, Norway. A total of 148 haddock larvae and 9 pollock larvae were used to examine increment formation. Because haddock and pollock eggs were indistinguishable; individuals were later identified by their larval characteristics.

Otolith preparation

A dissecting microscope illuminated with polarized light was used to dissect the sagittae and lapilli from larval skulls with the aid of fine needles. One thousand two hundred and sixty pairs of haddock and pollock larval otoliths from the validation experiment and from wild fish <36 mm SL were mounted on glass over slides with Permount (Fisher Scientific Laboratory, Fair Lawn, NJ). Eighteen pairs of haddock otoliths from larvae measuring 50–83 mm SL were mounted with synthetic resin on metal stubs for SEM observation.

The mounted otoliths (sagittae) used in the validation experiment were read with an image analyzer system by using Optimas software (Subtechnique, Inc., Alexandria, VA). Otoliths from field-collected larvae and juveniles were read at the Southwest Fisheries Center (La Jolla, CA) by using the OTO program (Andersen and Mokness, 1988). The image analyzer system consisted of a video camera attached to a compound microscope, monitor, digitizer, and microcomputer. A detailed description of the OTO program, otolith analyzing system, and methods used are given by Andersen and Moksness (1988). Otoliths examined with SEM were ground on the sagittal plane to the nucleus with fine grit paper (between 30 µm and 0.3 µm), and then the polished surface was etched for 6 min in 0.2M EDTA (pH 7.6).

In addition to the number of increments, the following otolith measurements were taken and used in comparisons of each species: maximum otolith diameter (OD); maximum otolith radius from the center of the nucleus to the outer edge of the otolith (OR); diameter of the otolith nucleus (ON); and diameter of the yolksac resorption check (YSC) as defined by Radtke and Waiwood (1980) and Bolz and Lough (1983). Growth increments were counted twice by the same reader at an interval of 3 mo between readings. The two counts usually differed <6%, and the average was used as an estimate of age.

Statistical procedures

For both species, of all otolith measurements, the maximum otolith diameter was most strongly correlated with length. I compared the relation of otolith growth to larval growth between month and year for both species to determine whether otolith growth could be used to predict larval growth. Thus, linear regressions of LnSL on LnOD were compared by using analysis of covariance (ANCOVA) with OD as the covariate.

A Laird-Gompertz growth model curve was fitted to the length-at-age data for each species in each year. This model has been shown to provide an adequate fit for length-at-age data on age 0+ fish of many different species (Bolz and Lough, 1988; Lough et al., 1982; Watanabe et al., 1988; Simard et al., 1992). Zweifel and Lasker (1976) presented a detailed discussion of the Laird-Gompertz function. The equation for the model is

$$L_t = L_0 e^{k(1-e^{-at})},$$

where L_0 = length at t=0;
k = a dimensionless parameter, such that $ka=A_0$ is the specific growth rate at t=0 ($A_t=A_0e^{-at}$);
L_t = length at any age t;
a = the specific rate of growth when $t=t_0$; and
t_0 = the time when the growth rate starts to decrease, that is, the inflection point of the curve (Ricker, 1979).

The parameters were derived by nonlinear least squares tests by using the SYSTAT nonlinear program (Wilkinson, 1990), and ANCOVA was used to test whether differences in growth rates in different years of each species were significant.

Results

Validation of daily increment deposition

In both species, otoliths (sagittae and lapilli) were present at hatching. Some haddock otoliths (Fig. 2A) showed one to three irregular increments between the nucleus and the check at hatching, as observed by Bolz and Lough (1983). The mean (±SD) diameters of the nucleus and of the check at hatching of reared larvae were 10.8 ±2.5 and 21.4 ±3.3 µm, respectively, in haddock and 12.0 ±1.9 and 20.7 ±2.2 µm, respectively, in pollock. The values for haddock were consistent with earlier reports by Bolz and Lough (1983) and Campana (1989). In both species, increments appeared as alternate light and dark zones (Fig. 2), and the first regular increment was formed the day after hatching (Table 2). The number of increments (NI) corresponded to the chronological age in d (AGE) of the larvae (Fig. 3). The slopes of the regressions for haddock (NI=0.99 AGE, n=148, r^2=0.96, P>0.0001) and pollock (NI=1.09 AGE, n=9, r^2=0.82, P=0.0005) did not differ significantly from 1 (t-test, P=0.637 for haddock and P=0.890 for pollock).

Growth of haddock and pollock otoliths

The check at hatching was clearly visible and increments were easily distinguished in the otoliths of larvae sampled at sea (Fig. 4). The nuclear and check diameters at hatching for haddock and pollock differed in different years (ANOVA, P<0.01) (Table 3). For haddock, differences in nuclear check diameters between 1991 and 1993 were not significant (ANOVA, P>0.05). There were no significant differences among years for yolksac check diameters for either haddock or pollock larvae (ANOVA, $P>0.05$). Within some haddock otolith nuclei, 1–3 increments were observed. Outside the nucleus, 6–8 growth increments of irregular width were observed between the nucleus check and a second well-marked check. Bolz and Lough (1983) observed 2–8 faint increments bounded by a discontinuous zone that appeared to be analogous to the yolksac check found in larval cod otoliths by Radtke and Waiwood (1980). Accordingly, I interpreted the second well-defined mark as a check resulting from yolksac resorption. The mean diameter of the yolksac check was 34.9 ±2.8 µm in haddock and 35.3 ±2.6 µm in pollock. Several (mean 7 ± 1.8) narrow (<1 µm) increments were found immediately after the yolksac resorption check. Increment width increased rapidly in subsequent increments.

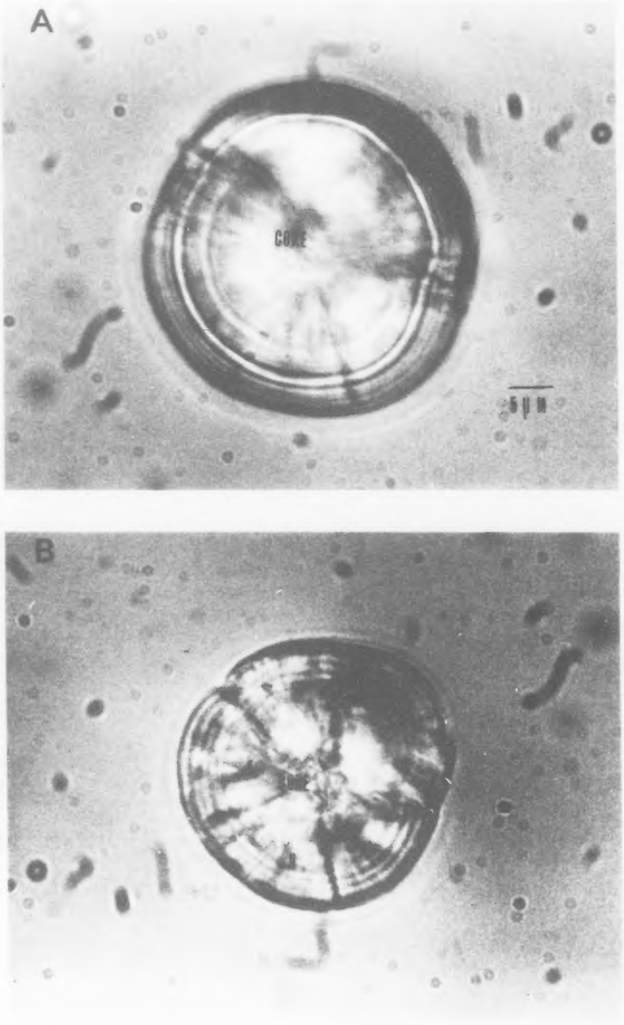

Figure 2

Light micrographs of sagittae. (**A**) Sagitta from a 5.93-mm, 5-day-old, haddock larva. (**B**) Saggita from a 4.98-mm, 3-day-old, pollock larva. H = hatch check. Growth increments appear as light and dark zones. The larvae were hatched from eggs collected from the Western and Emerald Banks area. Bar represents 5 µm.

The relation between otolith and larval fish sizes was best described by a ln-ln regression (Fig. 5). For haddock and pollock, significant differences were found between cruises (ANCOVA, $P<0.05$); however, no significant differences were found among years (ANCOVA, $P>0.05$) for either species (Table 4). Among haddock samples, a multiple range test revealed four homogeneous groupings in the samples from the ten cruises analyzed ($P<0.01$). The groupings were interpretable in terms of monthly sagittal growth. The first group integrated larvae from March to April; the second, larvae from May; the third, larvae from June; and the fourth, larvae from July. With pollock, the multiple range test showed three homogeneous groupings among the pollock sampled during the ten cruises ($P<0.01$). The first group integrated larvae from November to January; the second, larvae from February; and the third, larvae from March to April. It was possible to distinguish different stages in sagittal growth from otolith structure. Sagittae from the early developmental stages of haddock and pollock larvae were almost circular in shape, and there was one flat and one convex-side, accessory nucleus developed in the sagittae of postlarvae. As the larvae developed, the otoliths grew faster along the anteroposterior axis and became oval shaped.

Haddock and pollock larval and juvenile growth

For both haddock and pollock, the first otolith increment was laid down the day after hatching. Thus, the age of larvae and juveniles was indicated by the number of increments in the sagittae. Daily increments were counted in otoliths from 1121 individuals of a total of 3126 cap-

Table 2

Chronological age (from hatching), otolith diameter, and increment formation in reared larval haddock and pollock.

Chronological age (days)	Standard length (mm)	Otolith diameter (μm)	Increment	± SD	Number of larvae
Haddock					
0	4.69	26.70	0.5	0.5	18
1	4.75	27.87	1.1	0.2	15
2	5.12	30.04	2.1	0.3	21
3	5.16	32.11	3	0.4	15
4	5.68	33.03	4.1	0.4	26
5	5.74	34.03	5.1	0.3	13
6	5.86	34.04	5.8	0.6	23
7	5.90	34.41	6.6	0.8	9
8	5.86	36.45	7.3	0.4	4
9	5.77	36.92	8.5	0.5	2
10	5.84	37.58	10	—	1
11	6.19	37.67	11	—	1
Pollock					
0	4.10	24.72	1	—	1
1	3.81	26.10	1	—	1
2	4.34	29.38	2	0	3
3	5.00	28.78	3.3	0.5	3
4	4.49	32.49	4	—	1

Table 3

ANOVA of nucleus, hatching, and yolksac checks on year for haddock and pollock larvae collected on the Scotian Shelf.

		1991	1992	1993	*F*	*P>F*
Haddock	Nucleus[1]	15.7	16.9	15.5	40.8	0.00
	SD	1.4	1.3	1.4		
	Hatching	22.4	25.1	23.5	34.9	0.00
	SD	2.6	3	2.1		
	Yolksac	36.6	38.7	35	0.28	0.76
	SD	3.9	4.1	2.7		
Pollock	Nucleus		14.8	15.9	38.7	0.00
	SD		1.6	1.8		
	Hatching		23.9	23.1	38.1	0.00
	SD		1.4	1.9		
	Yolksac		35.6	35.1	5.2	0.02
	SD		2.6	2.7		

[1] Nucleus check 1991 versus 1993 not significant ($P>0.42$).

tured. Haddock larvae and juveniles (n=602) ranged from 2.7 to 83.0 mm in SL and from 0 to 128 d in age, and pollock larvae and juveniles (n=519) from 2.8 to 23.8 mm in SL and from 0 to 84 d in age. For each year, Gompertz growth curves were fitted to describe the mean growth of larval and juvenile haddock (1991, 1992, and 1993) and pollock (1992 and 1993) (Fig. 6; Table 5). Length at hatching predicted from the curves was 4.1 mm for haddock and 4.5 mm for pollock, both within the range reported by previous studies (Fridgeirsson, 1978; Bolz and Lough, 1983; Fahay, 1983). Because the predicted inflection point for both haddock and pollock curves fell beyond the length range analyzed, the end of the first growing season had not been reached.

Although haddock larvae older than 80 d were obtained in 1991 and 1992, they were not used in the comparison of growth. Haddock growth rates (mm/d) during the first 80-d period in 1993 were different from those in 1991, and growth rates in 1993 were different from those in 1992 (ANCOVA, $P<0.01$) (Table 6). The 1993 cohort had the lowest growth rate. The 1991 and 1992 cohorts had similar growth rates (ANCOVA, $P=0.84$). The average growth rate of larvae was 0.21 mm/d during the first month and 0.42 mm/d during the second month. Growth continued exponentially from the predicted length at hatching throughout the size range of larvae and juvenile collected, there being no indication of a cessation in growth.

Pollock growth rates (mm/d) varied significantly among years (ANCOVA, $P<0.01$) (Table 6). However,

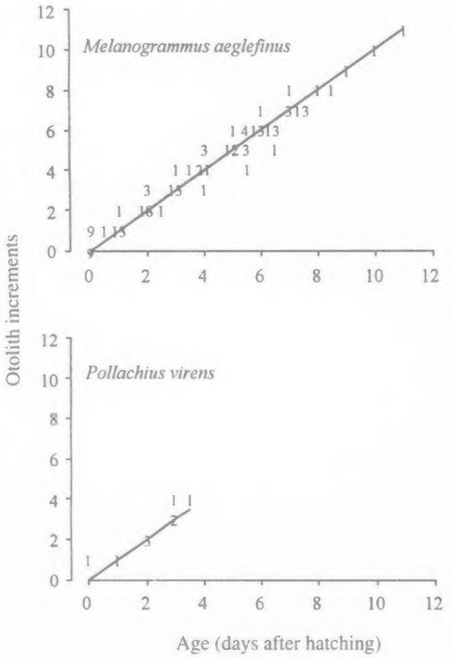

Figure 3

Number of increments enumerated on the sagittae of haddock and pollock larvae as a function of known age (days after hatching). Numbers represent the number of larvae. The number of increments (NI) corresponds to the chronological age in d (AGE) of the larvae. Haddock $NI = 0.99\ AGE$, $n = 148$, $r^2 = 0.96$, and pollock $NI = 1.09\ AGE$, $n = 9$, $r^2 = 0.82$.

the A_0 (specific growth rate at t=0) did not vary significantly (ANCOVA, P>0.05). The 1992 cohort had the higher growth rates during the first 50 d following hatching. Growth was linear at 0.18 mm/d following the predicted hatching size (1992 cohort), 0.13 mm/d (1993 cohort) through the first month, and 0.23 (1992 cohort) and 0.24 mm/d (1993 cohort) through the second month.

Discussion and conclusions

Validation of increment deposition

The present study shows that growth increments in haddock otoliths are formed daily and suggests that this is also the case in pollock. In both species, the first of the regular increments is formed on the day after hatching, and thereafter an additional increment is added each day up to 11 d for haddock and 4 d for pollock. Otoliths develop before hatching, and in haddock, 1 to 3 irregular increments are deposited prior to hatching. These types of irregular increments were not observed on larval otoliths of pollock. A few embryonic growth increments of a lamellar structure (such as I observed in haddock), have also been reported in other species (Brothers et al., 1976; Radtke and Dean, 1982; Watanabe et al., 1982; Nishimura and Yamada, 1984; Palomera et al., 1988). The spacing of embryonic increments is irregular, in contrast to regularly spaced posthatching increments, which indicates that they might not be deposited at daily intervals. Whereas Radtke and Waiwood (1980) did not observe increments formed prior to hatching in cod (*G. morhua)*, they did observe regular increments that were formed daily starting one day after hatching. Brothers and McFarland (1981) noted three diffuse increments in the otolith core of French grunt (*Haemulon flavolineatum*) and speculated that they were deposited during the embryonic stage. Bolz and Lough (1983) found 1–2 poorly defined increments enclosed by the nuclear check in haddock larvae. According to the above observations, it seems reasonable to infer that the 1–3 irregular increments inside the hatch check of haddock otoliths are formed sometime during the 2–3 week egg stage (Laurence and Rogers, 1976; Fridgeirsson, 1978).

Growth of haddock and pollock otoliths

The sagittal otoliths of haddock and pollock larvae are circular in shape at the age of 35–40 d. Subsequent sagittal growth is greater along the anteroposterior plane, so that the otoliths become oval shaped in older larvae. Radtke (1989) reported that cod (*G. morhua*) sagittae change as they grow, from spherical to elongated to crenulated over a 65-d period. In haddock and pollock larvae, circular-shaped sagittae were observed until 8 mm SL, corresponding to an age of 35–40 d. Then, the sagittal shape begins to elongate as the result of growth of peripheral primordia, which corresponds to 30 mm SL (75–80 d) in haddock and 23 mm SL (80 d) in pollock. Thereafter the sagittae are not easily broken, and their shape is distinguishable from that of other gadoid species. The last changes in otolith shape correspond to the age when juveniles undergo metamorphosis to begin demersal life. Koeller et al. (1986) inferred, from a series of midwater and botton trawl surveys conducted in 1983 off southwestern Nova Scotia, that the transition to the demersal habitat by haddock occurs from June to August.

In most otoliths examined, I observed a well-defined, dark and discontinuous zone or ring laid down

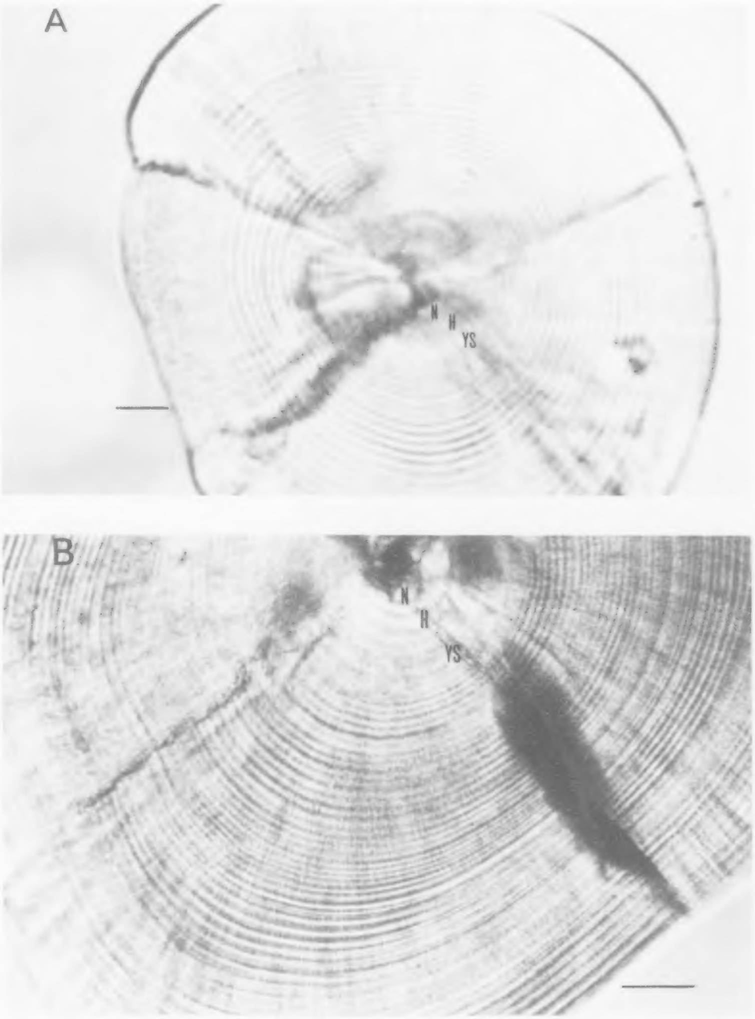

Figure 4

Light micrographs of sagittae showing different landmark checks. (**A**) Sagitta from a 13.7-mm-SL, 37-day-old haddock. (**B**) Sagitta from a 12.4-mm-SL, 50-day-old pollock. N = nuclear check, H = check at hatching, and YS = yolksac check. Bar of photograph represents 10 µm.

around the nucleus. It was the first mark presented in larval otoliths (Bolz and Lough, 1983; Radtke and Waiwood, 1980; Campana, 1989). Outside the nucleus, four to eight irregularly spaced increments were bounded by a discontinuous zone which appeared to be the yolksac check (Bolz and Lough, 1983). Laurence (1974) reported that at 7°C yolksac exhaustion occurs 6–7 d after hatching for haddock, and Fridgeirsson (1978) observed that at 7.2°C yolksac exhaustion occurs within 6 d for haddock larvae and 8 d for pollock larvae. From the regression of larval length to sagittal diameter, I estimated that yolksac resorption occurs at a standard length of 5.0 mm in haddock (at 3.5°C) and 5.1 mm in pollock larvae (at 5.0°C), corresponding to a mean age of 9 and 5 d, respectively. Fridgeirsson (1978) reported that haddock start independent feeding at 6–10 d after hatching and pollock at 8–10 d after hatching.

This suggests that the observed check is deposited at or immediately before yolksac absorption and that the number of increments between the nucleus and the absorption check reflects the duration of the yolksac phase (Fridgeirsson, 1978; Laurence, 1978; Fahay, 1983).

Haddock and pollock larval and juvenile growth

In recent years, the examination of otolith microstructure has resulted in many applications (Jones, 1992). The underlying assumption is that increments form daily. In otoliths of haddock (*M. aeglefinus*), and pollock (*P. virens*), increments are deposited daily and thus can provide accurate estimates of age (Bolz and Lough, 1983; Campana, 1989; Campana and Hurley, 1989).

The estimates of haddock growth in this study are comparable with those reported earlier. Thus, the predicted length of 4.1 mm at hatching and the average growth rate of 0.65 mm/d for 0–4 mo old larvae in the present study are similar to the values reported by Bolz and Lough (1983, 1988). The adjustment of a Laird-Gompertz model (r^2=0.99) for the entire data set correctly predicted length (Table 5). Different patterns in growth occur during ontogeny (Table 6). The average increase in length is moderate between hatching and 50 d (0.27 mm/d), high for early juveniles of 2.5–3 mo (0.68 mm/d), and moderate again (1.2 mm/d) for older juvenile. Few studies provide estimates of the age and growth of larval and juvenile pollock (Campana, 1989). The predicted length at hatching was 4.5 mm and the average growth rate of larval was 0.22 mm/d during the first 3 mo. The Laird-Gompertz model (r^2=0.98) applied to the entire set data adequately described growth. A slow increase in length occurs during the first 30 d after hatching (0.18 mm/d), and then the rate is moderate during the following 1 to 2 mo (0.23 mm/d). Finally, a stable period (0.24 mm/d) begins (Table 6). In the present study only the pelagic phase prior to metamorphosis and beginning of demersal life was examined. Nevertheless, sampling continued throughout the year and older pollock juveniles up to 80 d old (23 mm SL) were captured. The last pollock samples were collected in 1993. Juvenile pollock probably move from the oceanic zone to the shallow coastal zone after metamorphosis (Scott and Scott, 1988). Campana (1989) collected 53 pollock juveniles from the north shore of Gran Manan Island, New Brunswick, on August 1984, and the mean length of juveniles was 97.3 ± 1.9 mm. The date of capture of Campana's samples suggest that pollock juvenile move to the Scotian shore, possibly toward the Bay of Fundy, to finish their development. If pollock sharply increase their growth rate in response to improved feeding conditions during demersal lifestyle, as we observed for haddock, they could attain an average length of 106 mm by August, a size similar to that of juveniles collected by Campana. Growth rates (mm/d) varied significantly in different years, and the rates of the two cohorts showed an alternate pattern: growth was higher for the 1992 cohort during the first 45 d and higher for 1993 cohort following the first 45 d. The 1993 cohort was first detected two months later than the 1992 cohort. The adjustment of a Laird-Gompertz model (r^2=0.98) to each annual data set closely predicted length (Table 5).

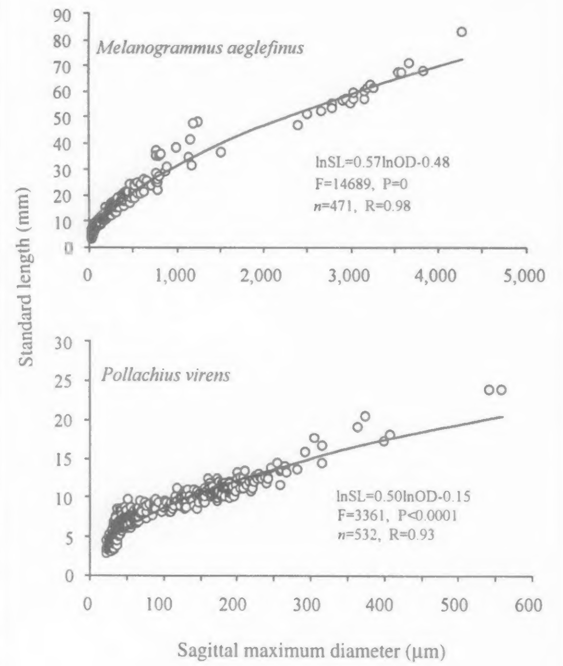

Figure 5

Standard length as a function of maximum sagittal diameter in larval pollock and haddock.

Growth during the juvenile period of haddock and pollock can be divided into a series of "stanzas." The change from one stanza to the next is characterized by a discontinuity in development, such as during hatching or after a change of habitat (Ricker, 1979). Growth accelerates abruptly in fish older than 50 d in response to a shift from a pelagic to a demersal diet. Because we captured juvenile pollock immediately after the transition

Table 4

Parameter estimates of the relationship between standard length and sagittal diameter for larval haddock and pollock collected on the Scotian Shelf. $\text{Ln}SL = a + b\text{LnSD}$. Note: The reduced correlation during March 1992 and 1993 for larval haddock is the result of differences between size of larvae and sagittal diameter at hatching.

			Intercept (a)		Slope (b)			
Species	Year	Month	Estimate	SE	Estimate	SE	n	r^2
Haddock	1991	June	0.006	0.090	0.477	0.014	37	0.97
		July	–3.140	0.442	0.898	0.055	18	0.94
	1991		–0.524	0.077	0.567	0.011	55	0.98
	1992	March	0.840	0.781	0.157	0.216	12	0.05
		April	–0.998	0.422	0.705	0.120	12	0.77
		May	0.068	0.101	0.466	0.022	65	0.87
		June	–0.002	0.167	0.500	0.027	16	0.96
		July	–0.722	0.530	0.594	0.078	5	0.95
	1992		–0.466	0.059	0.572	0.012	110	0.95
	1993	March	–4.574	0.467	1.733	0.134	134	0.56
		April	–0.618	0.162	0.612	0.038	45	0.86
		May	0.047	0.056	0.466	0.011	127	0.94
	1993		–0.469	0.032	0.564	0.007	306	0.95
		All	–0.445	0.021	0.560	0.004	471	0.97
Pollock	1991	November	2.162	0.239	–0.224	0.069	4	0.84
		December	–0.646	0.409	0.613	0.113	12	0.75
	1992	January	–0.943	0.154	0.717	0.041	91	0.77
		February	–0.095	0.093	0.482	0.019	80	0.89
		March	–1.011	0.325	0.644	0.060	17	0.88
		April	–0.463	0.469	0.568	0.087	7	0.90
	1991–1992		–0.143	0.045	0.494	0.010	211	0.92
	1993	January	–0.932	0.132	0.720	0.036	258	0.60
		February	0.694	0.119	0.326	0.024	54	0.78
		March	–0.856	0.334	0.632	0.060	5	0.97
		April	–0.392	0.505	0.538	0.091	4	0.95
	1993		–0.204	0.057	0.517	0.015	321	0.80
		All	–0.143	0.036	0.498	0.009	532	0.86

to a demersal life stage, it was possible that individuals were present in both pelagic and demersal zones at this time. Perhaps pollock juveniles were moving from the oceanic to the coastal zone; if so, this change in habitat could explain the reduction in numbers of juvenile older than 60 d in our sampling. I assume that conclusions drawn for juvenile haddock are valid only during the first eighty days for pollock. This period corresponds to the transition from a primarily pelagic to predominantly demersal life stage, which occurs when haddock reach about 20–25 mm in length (Koeller et al., 1986) and when pollock reach 10–15 mm. Although >25-mm haddock were captured in the water column, they probably had adopted a predominantly demersal life style. Thus, the acceleration in growth of >50-d juveniles could have reflected exploitation of abundant food resource after settling on the bottom (Mahon and Neilson, 1987).

Table 5

Estimates of Gompertz model parameters for larval and juvenile haddock and pollock collected on the Scotian Shelf. L_0 = lenght at age $t = 0$, a = specific rate of growth at $t = t_0$, and k=dimensionless parameter.

Species	Year	L_0	a	k	n	r^2
Haddock	1991	2.478	0.010	4.954	114	0.99
	1992	3.609	0.006	6.172	107	0.99
	1993	4.317	0.005	5.809	381	0.99
	All	4.198	0.005	6.581	602	0.99
Pollock	1991–92	4.213	0.013	2.483	210	0.99
	1993	4.617	0.017	1.970	309	0.98
	All	4.569	0.013	2.429	519	0.98

In the present study, average growth rates were 0.21 mm/d in the first month and 0.42 mm/d in the second month for larval haddock and 0.18 mm/d in the first month and 0.23 mm/d in the second month for larval pollock. Growth continued exponentially

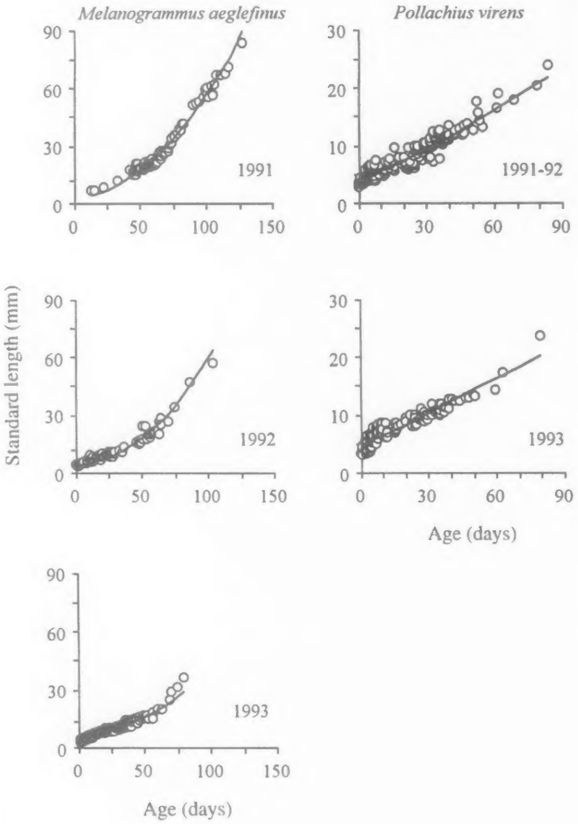

Figure 6

Estimated age versus length for larval and juvenile pollock and haddock. Lines were fitted by using the Laird-Gompertz growth model. Parameters of the model are shown in Table 5.

from the predicted length at hatching throughout the size range of larvae and juvenile collected. Otolith growth increments are suitable for estimating age, and the analysis of length–age data for young haddock and pollock on Emerald and Sable Island Banks suggests that the growth rate increases sharply at the transition from a pelagic to demersal life stage. Thus, pelagic and early demersal growth likely represents distinct “stanzas” in the growth history of these gadoids, and these “stanzas” may have different effects on recruitment variability. Rapid juvenile growth may increase juvenile survivorship by decreasing the time during which juvenile are exposed to predators (Houde, 1987). Interannual variation in juvenile growth rates may influence interannual variation in juvenile survivorship. Additional complicating factors during the pelagic phase of juvenile fish, such as different residence times and diel migrations in the water column (Koeller et al., 1986), reduce the possibility of identifing correlations between interannual variation in growth rates and environmental factors, and thereby allow predictions of recruitment success.

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Table 6

Growth rate (mm/d and %/d) of larval and juvenile haddock and pollock estimated from the Laird-Gompertz growth model.

Age (days)	Haddock								Pollock					
	Growth rates (mm/d)				Growth rates (%/d)				Growth rates (mm/d)			Growth rates (%/d)		
	1991	1992	1993	All	1991	1992	1993	All	1992	1993	All	1992	1993	All
0	0.13	0.13	0.11	0.14	4.00	3.70	2.56	3.85	0.14	0.10	0.14	3.23	1.85	3.16
5	0.16	0.16	0.12	0.16	3.86	3.59	2.56	3.72	0.15	0.10	0.16	3.02	1.85	2.96
10	0.18	0.18	0.14	0.18	3.73	3.49	2.56	3.59	0.16	0.11	0.17	2.83	1.85	2.77
15	0.21	0.21	0.16	0.21	3.60	3.38	2.56	3.47	0.17	0.13	0.18	2.66	1.84	2.60
20	0.24	0.24	0.18	0.24	3.48	3.28	2.55	3.35	0.19	0.14	0.19	2.49	1.84	2.43
25	0.28	0.27	0.21	0.27	3.36	3.19	2.55	3.23	0.20	0.15	0.20	2.33	1.84	2.28
30	0.32	0.31	0.24	0.31	3.24	3.09	2.55	3.12	0.21	0.16	0.21	2.19	1.84	2.14
35	0.36	0.35	0.27	0.35	3.13	3.00	2.55	3.01	0.21	0.18	0.22	2.05	1.84	2.00
40	0.40	0.39	0.31	0.39	3.02	2.91	2.55	2.91	0.22	0.20	0.23	1.92	1.83	1.88
45	0.45	0.44	0.35	0.44	2.92	2.83	2.55	2.81	0.23	0.22	0.24	1.80	1.83	1.76
50	0.50	0.49	0.40	0.48	2.82	2.74	2.55	2.71	0.23	0.24	0.24	1.69	1.83	1.65
55	0.56	0.54	0.45	0.53	2.72	2.66	2.55	2.62	0.24	0.26	0.24	1.58	1.83	1.54
60	0.62	0.60	0.52	0.59	2.63	2.58	2.55	2.53	0.24	0.28	0.25	1.48	1.82	1.45
65	0.68	0.66	0.59	0.64	2.54	2.51	2.55	2.44	0.24	0.31	0.25	1.39	1.82	1.36
70	0.74	0.73	0.67	0.70	2.45	2.43	2.55	2.36	0.24	0.34	0.25	1.30	1.82	1.27
75	0.81	0.80	0.76	0.76	2.37	2.36	2.55	2.28	0.24	0.37	0.25	1.22	1.82	1.19
80	0.88	0.87	0.86	0.82	2.29	2.29	2.55	2.20	0.24	0.41	0.25	1.14	1.82	1.12
85	0.95	0.94		0.88	2.21	2.22	2.12	0.24		0.24		1.07		1.05
90	1.02	1.02		0.94	2.13	2.16	2.05							
95	1.09	1.10		1.01	2.06	2.09	1.98							
100	1.17	1.19		1.07	1.99	2.03	1.91							
105	1.24	1.27		1.14	1.92	1.97	1.85							
110	1.32			1.20	1.85		1.78							
115	1.39			1.27	1.79		1.72							
120	1.47			1.33	1.73		1.66							
125	1.54			1.40	1.67		1.61							
130	1.62			1.46	1.61		1.55							

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Abstract.—We used hydroacoustic techniques to obtain biomass estimates of yellowtail rockfish, *Sebastes flavidus*, in a 100-km^2 area off the west coast of British Columbia, Canada. The purpose of our study was to estimate sampling variance and explore the effect of diel aggregation behavior on the precision of biomass estimates. A set of eight transects was sampled eight times: four at night, four during daylight. Although we observed a pronounced diel behavioral pattern of diurnal aggregation and nocturnal dispersion, we found no significant differences between nocturnal and diurnal estimates of mean biomass. Diurnal estimates showed a tendency towards higher variance, but the differences were not significant in most comparisons and were too small to influence survey design. The coefficient of variation of the eight observations for any individual transect ranged from 13 to 128%. The coefficient of variation in biomass for the whole survey area, based on repeating the set of eight transects eight times, was 13.9% and the estimate of mean biomass for the survey area was 1152 t. The observed diel behavioral patterns did not, in this study, produce different estimates of yellowtail rockfish biomass. Survey time might therefore be optimized without concern for this source of variance for this species.

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Diel vertical migration by yellowtail rockfish, *Sebastes flavidus*, and its impact on acoustic biomass estimation

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Yellowtail rockfish, *Sebastes flavidus*, are an important component of the British Columbia (B.C.) trawl fishery. Annual catches of 4000–5000 t represent about 20% of the total rockfish (*Sebastes* spp.) landings and over 5% of the total domestic trawl landings from the B.C. coast (Rutherford, 1996). The stock assessments for these species have typically relied upon population dynamics models tuned with catch-per-unit-of-effort indices (Stanley, 1993) or swept-area surveys (Leaman and Stanley, 1993). However, problems with both these methods have led us to investigate more direct methods.

Previous hydroacoustic work indicated that some of the trawl-caught rockfishes are aggregating species and that they are usually found associated with specific bathymetric features (Wilkins, 1986; Leaman et al., 1990; Kieser et al., 1992; Richards et al., 1991). Submersible observations and acoustic tagging of a small number of fish confirmed this association for yellowtail rockfish (Pearcy et al., 1989), although the acoustic tagging did not indicate consistent diel patterns (Pearcy, 1992). This aggregating behavior off the bottom in predictable locations suggests that this species may be a suitable candidate for hydroacoustic biomass estimation. However, because individual yellowtail rockfish stocks are thought to occupy large areas (Stanley, 1993; Stanley et al., 1994), such comprehensive hydroacoustic surveys would be costly and time-consuming. This accentuated the need for a prior study of fish behavior and sampling variance to assess the feasibility of such an approach and to optimize survey effort. We were also concerned about the impact of diel aggregating behavior on the precision and bias of biomass estimates (Olsen, 1990; Appenzeller and Leggett, 1992; Simmonds et al., 1992). Within the same genus, Richards et al. (1991) reported strong diurnal aggregation by Pacific ocean perch (*S. alutus*), and Wilkins (1986) has reported strong nocturnal aggregation by widow rockfish (*S. entomelas*).

We investigated these issues with an experimental survey in November 1991 in waters 10 km west of Vancouver Island, British Columbia, Canada (Fig. 1). The objective was to estimate yellowtail rockfish abundance within a small area and, in doing so, to examine the variance within and among transects. In addition, we wished to characterize diel patterns of behavior and document the effects of such behavior on the precision of the biomass esti-

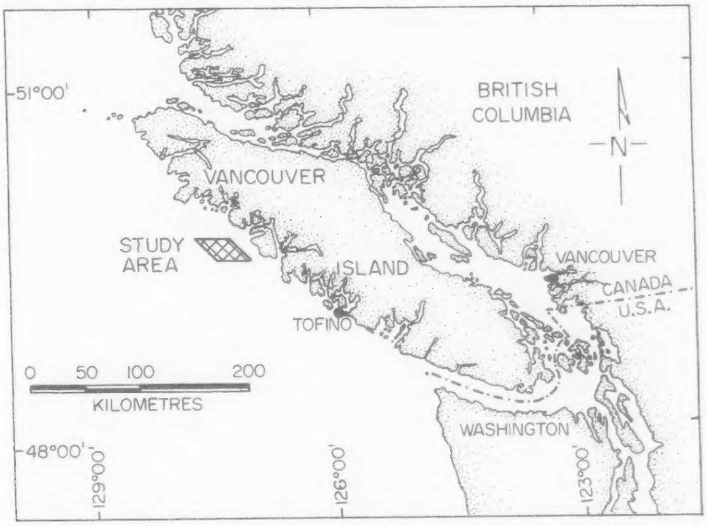

Figure 1

Location of study area off the southwest coast of Vancouver Island, British Columbia, Canada.

mates. In this report, we summarize our observations from this study and discuss the implications of the results to hydroacoustic survey design for yellowtail rockfish.

Methods

Study area

We first surveyed a 250-km^2 area along the shelf edge off Nootka Island to locate concentrations of rockfish (Fig. 1). This area produces 1000–3000 t of yellowtail rockfish per year (Rutherford, 1996). An initial grid included nine parallel transects 9–13 km in length and 2.8 km apart. They were oriented southwest to northeast, perpendicular to the isobaths. The southwestern end of the track lines extended well beyond the shelf break, whereas the shallower northeastern end extended onto the shelf to the 130-m isobath. This A series was covered during one 24-h period. The northern half of the A series showed the greatest concentrations of rockfish. From this northern area, we selected a B series of transects to conduct the study (Fig. 2). No further use was made of A-series measurements because the respective transects were not comparable with the B-series transects. The distance between transects was halved to 1.4 km, and the length of each was reduced to span depths from the 140-m isobath to just beyond the shelf break (180 m). The A series had shown that essentially all fish concentrations were between these limits. The B series was repeated in the same sequence (B9–B2) through four 24-h cycles to produce a balanced design of four diurnal and four nocturnal observations per transect. In addition to the acoustic estimates for the eight replicates of B2–B9, we selected B5 and B6 for continuous soundings, resulting in ten additional observations for these two transects.

The bottom topography of transects B2–B9, with the exception of B8, was characterized by one or two underwater cliffs They appeared to be 10–15 m high and followed a north–south axis through the study area, landward of the shelf break (Figs. 2–4). The transects were oriented perpendicular to the axes of the cliffs. At the southernmost transect (B9), the cliffs were approximately 1.5 km inshore of the shelf break. This distance increased to about 7.0 km by transect B2. The cliffs were found at a progressively shallower depth. This topographic feature is well known to fishermen as the “clay bumps” on the Nootka fishing grounds. Fishermen report that catches of yellowtail rockfish can be made year-round by towing bottom trawl nets in an east to west (shallow to deep) direction over the cliffs. Transect B5 corresponds to a commonly used commercial fishery tow (Figs. 2–4).

We excluded the results of transect B1 from our analyses. It passed over an extended underwater ridge such that the modal depth was less than 130 m rather than the targeted depth of 150 m. These depths are shallower than the November habitat

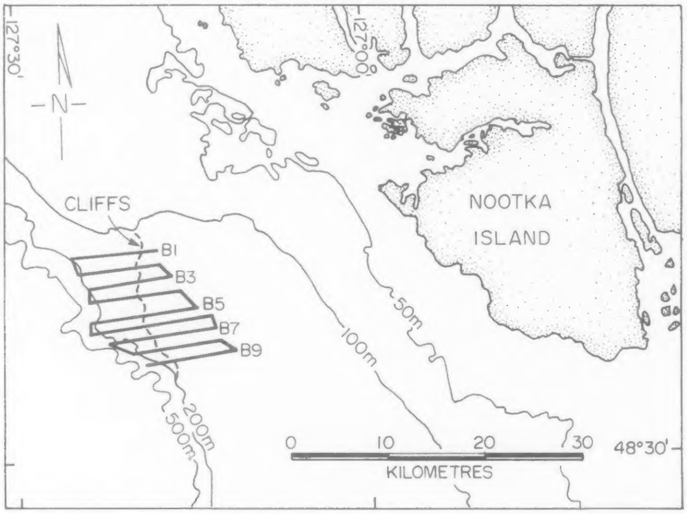

Figure 2

Area covered by the B-series transects and location of the shelf edge (200 m) and the cliffs in relation to the study area.

range for yellowtail rockfish (Nagtegaal, 1983). We also had to exclude the third of the four nocturnal replicates of transect B4. The vessel had to slow and change course to avoid traffic, leading to an unusable acoustic estimate. We used an average from the other three nocturnal estimates in our principal analyses to maintain a balanced ANOVA design. We also substituted a range of values in place of the missing value to examine the stability of the results.

Constant transects allowed us to compare behavior over the same location, but in doing so we sacrificed the improved statistical power we would have achieved with a stratified random design (Jolly and Hampton, 1991).

Time of the transect was classified according to the moment the vessel passed over the cliffs, the observed center of fish abundance. These times were then classified as diurnal or nocturnal according to the time of sunrise and sunset for Tofino, approximately 100 km southeast of the study area (Atmospheric Environment Service, Environment Canada).

Transect length

We derived two density estimates, based on a short and a long section from each completed transect, to examine the impacts of the choice of endpoints. For both sections and for each transect, we chose a standard beginning and end in relation to the cliffs (Fig. 3). The ends for the short sections of the transects were defined as the shoreward and seaward limits of the nocturnal dispersion of the cliff aggregations, judged visually from the echograms for all replicates. An individual transect required about one hour to complete. For these sections, the seaward end was inshore of the shelf break. The long sections used the same shoreward or shallow end, whereas the seaward or deep end was extended to a 180-m bottom depth. This depth incorporated the apparent deep-water limit of the shelf break aggregations (Fig. 3). The echograms for replicate transects (Fig. 3) differ in length because of differences in vessel speed over the ground. We calculated an average surface density (g/m^2) based on the constant length for each replicate of the short and long sections from all transects.

Hydroacoustic equipment and echo processing

Echo integration was used to estimate fish abundance in the survey area (Forbes and Nakken, 1972; Clay and Medwin, 1977; Foote, 1987; MacLennan and Simmonds, 1991). The calibrated echo integration system was operated from the Canadian Coast Guard Ship, *W. E. Ricker.* The acoustic processing equipment consisted of a BioSonics 38 kHz Model 101 echo sounder, BioSonics Model 111 chart recorder, BioSonics Model 121 digital echo integrator, PCM/VCR tape recording system, and auxiliary equipment. The transducer components included a towed body with a Simrad ceramic transducer and armored tow cable.

The echo integrator was programmed to analyze the return echoes for a series of depth strata (range slices) from the transducer to the bottom (Kieser et al., 1987). Bottom tracking was obtained with a 5-m bottom buffer. An echo integration sequence was completed every 60 pings (1 minute), and the measured echo intensities were stored on a personal computer. Echo integrator and chart recorder thresholds were set to 0.2 V; time-varied gain (TVG) was set to 20 log R. Thus all integrated echoes were displayed on the echogram. At this threshold level, noise was negligible at all depths of interest. Vessel speed was approximately nine knots.

The integrator output was processed with custom software to exclude extraneous signals from the ocean bottom, as well as noise and echoes from other unwanted sources in the water column.

A target strength (TS) of −32 dB/kg was used to convert the measured backscatter cross section to fish volume density (g/m^3) and fish surface density (g/m^2) estimates. This value was obtained from a review of the literature (Foote, 1987; Kieser, 1992); no *in situ* rockfish TS were available at that time. Only a relative TS was required because the study focused on the acoustic availability of rockfish and relative rather than absolute biomass and variance estimates.

Biomass estimates were obtained by extrapolating surface densities to cells that were bounded by lines equidistant between adjacent transects and by lines perpendicular to the transect and passing midway between measurements. An estimate of the total fish biomass for the area was obtained by summing the products of surface densities and cell areas.

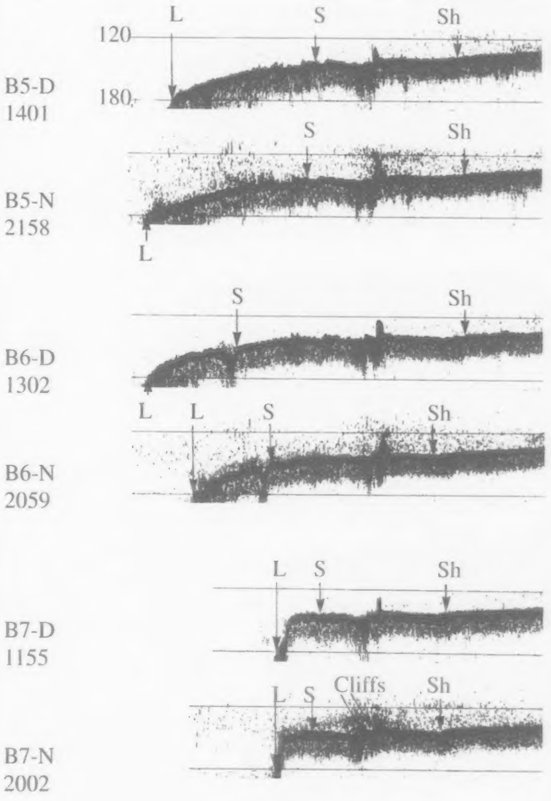

Figure 3

Diurnal (D) and nocturnal (N) echograms from transects B5, B6, and B7 for November 17. "Sh" identifies the shallow end of both long and short transects. "S" and "L" identify the deep ends of the short and long sections of the transects. Time shown represents the approximate time the vessel passed over the cliffs.

Fishing and sampling

We conducted three bottom trawl tows (Table 1). Two were conducted along the path of transect B5 and the other along transect B6. All three targeted diurnal aggregations at the cliffs. The tows ran from shallow to deep and were terminated at the seaward side of the cliffs, prior to encountering the aggregations near the shelf break. Planned additional bottom and midwater trawl fishing was curtailed owing to operational difficulties aboard the vessel.

Analysis of variance

Transect series 1, 2, 3, and 4 were conducted 17–18, 20–21, 22, and 24–25 November (Table 2). We initially tested for diel, transect, and series effects with a three-factor ANOVA:

$$\overline{D}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \varepsilon_{ijk},$$

where $\overline{D}_{ijk}$ = surface density for transect i, day or night j, and observation (or series) k;
μ = the overall mean;
α_i = the transect effect;
β_j = the diel effect.
γ_k = the influence of the date (series); and
ε_{ijk} = the error term, normally distributed with a mean of 0 and variance of σ^2.

To test whether diel variances were heterogeneous, we conducted a one-way randomization ANOVA limiting the factors to the diurnal-nocturnal effect. We conducted this test on a scaled version of the observations. Because it was obvious that the variance among transects was, in part, proportional to the mean, we removed the transect effects by scaling all the observations. Each observation was multiplied by the overall mean for the data set (n=64) divided by the mean for all eight observations (diurnal and nocturnal) of the transect. Thus the variation in the data set was reduced to the scaled "within transect" and diel effects.

Following examination of the balanced treatment of all transects, we examined the observations for transects B5 and B6 (Table 3). These data included observations from the four series as well as additional nonpaired observations. The two transects were examined separately. Homogeneity of variance between diel periods was examined by using an F-ratio test.

We used nonparametric randomization tests (Manly, 1991) to examine the sources of variance owing to concern about the small sample sizes, non-normality, and heterogeneity of variance. In particular, we hypothesized that variance among repeated transects would be proportional to the biomass estimates and, owing to the extreme densities and localization of the diurnal aggregations, that diurnal variance would be significantly greater than nocturnal variance.

Randomization involves resampling without replacement from one parent population. The observed value of the response statistic (for example, mean diurnal biomass minus mean nocturnal biomass) is compared with a large number of responses generated by treating all observations (diurnal and nocturnal) as coming from one parent population. Each of 4999 resamplings randomly allocates the observations into two groups, each time simulating new diurnal and nocturnal sets. The observed difference in mean biomass is then compared with the 4999 simulated differences. If the observed difference in biomass is significant (α<0.05), then the observed difference should be greater than 95% of all the simulated differences.

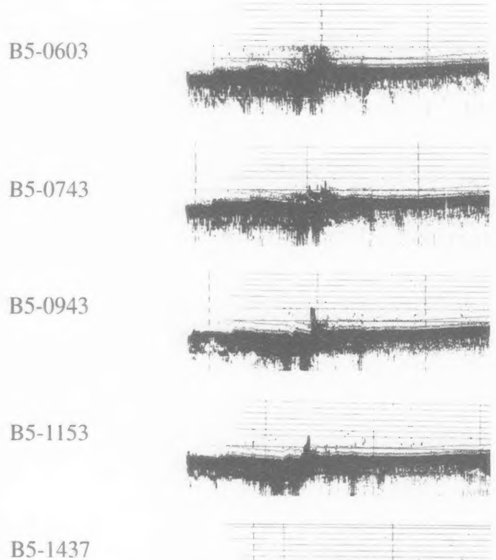

Figure 4

Echograms of transect B5 over 12 hours showing dawn and dusk transition of fish distribution over the cliffs. Time shown represents the approximate time the vessel passed over the cliffs.

Results

Fish behavior and species composition

Four aggregation types were observed on the echograms. Each was associated with a different habitat. The first, our targeted group, was located near the cliffs over depths of 150–160 m (Fig. 3). These dense schools were located near the bottom during each day, then the fish dispersed vertically and horizontally at twilight. By early nighttime, the scattered targets were distributed from 80 to 150 m. The diel cycle was completed by downward migration and rapid reformation of schools at dawn.

With the exception of benthic species like flatfish, which produce a negligible contribution to the acoustic measurement, the species composition in the catch from this aggregation type was over 85% yellowtail rockfish in the three tows (Table 1), indicating that this species dominated in the diurnal aggregations targeted near the cliffs. The continuous transition from day to night distributions (Fig. 4) implies that the nocturnal aggregations were also yellowtail rockfish, but it was not possible to confirm this assumption during the cruise. Subsequent discussions with fishermen familiar with nighttime trawling in the area supported the assumption that the nocturnal

Table 1

Catch composition (%) by weight and by species from diurnal bottom trawl tows ("tr" signifies trace, <0.05%).

	Tow			
	1	2	3	Total
Rockfish				
Silvergray rockfish (*Sebastes brevispinis*)	3.8	4.6	7.7	4.0
Widow rockfish (*S. entomelas*)	0.9	0.5	1.3	0.8
Yellowtail rockfish (*S. flavidus*)	88.2	83.2	38.5	85.9
Bocaccio (*S. paucispinis*)	7.1	2.8	tr	6.2
Other rockfish (*S.* spp.)	tr	tr	3.8	0.2
Other species (with swimbladders)	tr	0.3	2.6	0.1
Other species (without swimbladders)	tr	8.4	46.2	2.8
Total catch (kg)	1989	393	78	2460

Table 2

Biomass estimates (t) for the short and long sections of the transects ("na" indicates not available, measurement aborted owing to vessel traffic).

	Series							
	1		2		3		4	
Transect	Short	Long	Short	Long	Short	Long	Short	Long
Day								
2	93	119	65	70	96	104	170	188
3	162	162	228	232	114	118	103	106
4	98	99	37	50	126	134	46	60
5	124	130	84	92	124	136	92	124
6	424	448	520	522	32	32	396	402
7	148	148	39	40	186	194	111	116
8	4	4	58	58	161	208	18	20
9	187	187	209	278	296	345	118	123
Night								
2	181	200	112	124	116	123	59	68
3	92	113	152	166	85	90	124	134
4	56	112	77	103	na	na	74	84
5	128	230	112	162	128	180	92	100
6	156	216	150	180	476	512	128	144
7	198	212	114	138	224	235	229	241
8	185	224	142	169	131	173	146	157
9	76	126	178	202	240	357	168	208

targets would probably have been yellowtail rockfish. Commercial fishery records from these fishing grounds consistently indicate a predominance of yellowtail rockfish in midwater and bottom trawl tows.

The daytime tows support the assumption that the aggregation over the cliff was that of yellowtail rockfish, and the nocturnal dispersion of these aggregations is obvious from the night transects. These aggregations appear almost as dense as the bottom on our daytime echograms. The cliffs can be identified only in the echogram during the night (Figs. 3 and 4). We are not, however, suggesting that all fish in the transect were yellowtail rockfish, nor are we suggesting that the diurnal aggregations at the cliff represented all the yellowtail rockfish that were present in the transects. The nocturnal "cloud" may have included fish that were close to the bottom but not adjacent to the cliffs.

Figure B6-N indicates that there was some movement from off the edge onto the long and short ver-

Table 3

Biomass estimates (t) for the short and long sections of B5 and B6 (all observations).

			Series										
	Type	Transect	—	1	2	3	4	—	—	—	—	—	—
Day	Short	5		124	84	124	92	64	182	116	610	38	
	Long	5		130	92	136	100	172	182	132	632	332	
	Short	6		424	520	32	396	300	500	312	92		
	Long	6		448	552	32	402	308	508	320	124		
Night	Short	5	136	128	112	128	92	28	170	120	102	132	
	Long	5	188	230	162	180	124	28	212	156	140	288	
	Short	6	170	156	150	476	128	238	212	240	176	294	244
	Long	6	192	216	180	512	144	272	256	262	232	244	280

sions of the transect, suggesting some added contamination; however most of the backscatter was still concentrated near the cliffs.

A second aggregation type was represented by the schools observed at the shelf break, 10–20 m deeper than the base of the cliffs (Fig. 3). These schools, although exhibiting diel behavior similar to that of the first group, remained closer to the bottom during daytime. The greater depth of the aggregations (160–180 m), their closer proximity to the shelf edge, and their stronger bottom affinity suggested to us, as well as to various fishermen with whom we consulted, that these aggregations probably consisted of a combination of Pacific ocean perch (*S. alutus*), canary (*S. pinniger*), redstripe (*S. proriger*), sharpchin (*S. zacentrus*), and silvergray (*S. brevispinis*) rockfish (Leaman and Nagtegaal, 1982, 1986; Leaman et al., 1990).

The third and fourth target types included small schools or individual targets within the shallow end of the transects and scattered distributions over much deeper water beyond our transects and the shelf edge. The shallower signals were thought to be plankton or small fishes. Fishermen reported that attempts to fish on these aggregations were unsuccessful and suggested that the source of the signals was too small to be retained by their gear. No *in situ* target strength measurements were conducted. Signals in deeper water, off the edge of the shelf break, have been shown in other studies to be a deep plankton layer or hake (*Merluccius productus*) (Saunders[1]). Signals close to the slope off the edge could also be generated by side echoes.

Analysis of variance

The randomization tests provide the percent of the random re-orderings that exceed the value of the observed response. Statistical significance is assumed when fewer than 5% of the re-orderings exceed the observed response. The three-factor ANOVA indicated for both short and long transect sections (Table 4) that

1 there was no significant difference in mean biomass between night and day;
2 there was a highly significant difference in mean biomass among transects; and
3 there was no significant difference in mean biomass among different series (over time).

Table 4

Results of three-factor randomization ANOVA (df=degrees of freedom; **>1% significance level). Percentages indicate the % of 4999 random combinations of the observed data which resulted in a difference between treatments greater than the observed difference.

		% greater than observed	
Factor	df	Short section	Long section
Diurnal and nocturnal	1	87.94	47.40
Transect	7	**0.08	**0.08
Series	3	80.50	66.89
Error	53		
Total	64		

Bartlett's test for homogeneity of variance indicated no significant difference between the variance of diurnal and nocturnal observations, although the trend was towards greater diurnal variance (Table 5).

We repeated the same basic analysis using the larger but nonpaired set of observations for transects B5 and B6 (Table 3). Each transect was analyzed separately to test for significant differences between diurnal and nocturnal mean biomass and for homo-

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[1] Saunders, M. 1991. Pacific Biological Station, Nanaimo, B. C., Canada V9R 5K6. Personal commun.

Table 5

Results of Bartlett's test for significant difference between variance of diurnal and nocturnal observations (χ^2 for P=0.01 is 2.706; χ^2 for P=0.05 is 3.841).

	Short section	Long section
χ^2	2.45	2.23

geneity of variance between the two diel periods (Table 6). These data included the observations from the comparisons above; therefore, the data sets and tests are not independent of the main ANOVA.

Results for the short segments for B5 and B6 also showed no significant differences between mean nocturnal and diurnal biomass. However, unlike the results of the expanded B5 data set and the original all-transect test, diurnal variance for B6 was significantly higher than nocturnal variance for this transect.

Missing observation

The impact of using an average value (69 t) for the missing nocturnal observation was examined by conducting the randomization tests with minimum and maximum values of 56 t and 76 t for the nocturnal observations from B4. The alternate values had a negligible impact on the results.

Nocturnal dispersion beyond the shallow end of the transect

During one night series, the echograms indicated that the cliff aggregations dispersed beyond our empirically chosen shallow endpoint in transects B5–B9. We therefore slightly underestimated the nocturnal abundance of the cliff aggregations this one night. We re-analyzed the biomass for these transects with the new endpoints and then repeated the statistical analyses for the B2–B9 and B5–B6 series only. The changes to the one night's observations did not affect the results significantly.

Variance in transect and total biomass estimates

Independent total biomass estimates for the study area were estimated as the sum of the transect biomass estimates from each series (Table 7) . The overall average was 1152 t with a CV of 13.9% among series for the short sections. For the long sections, the average was 1329 t with a CV of 15.4%. The within-transect CVs ranged from 16.6% to 65.8% for the eight transects (short sections).

Table 6

Results of comparison of expanded observation set from transects B5 and B6 (* indicates > 5% level of significance). Percentages indicate the % of 4999 random combinations of the observed data which resulted in a difference between treatment means greater than the observed difference in means.

		% greater than observed	
Transect	Factor	Short section	Long section
5	Diurnal and nocturnal	35.79	22.54
	F-ratio	16.08	15.90
6	Diurnal and nocturnal	5.28	10.08
	F-ratio	16.10	1.60*

Table 7

Coefficients of variation of biomass estimates ($\hat{B}$) among transects and series (short and long sections).

		Short section		Long section	
Area	n	$\hat{B}$(t)	CV%	$\hat{B}$(t)	CV%
Total area					
Day	4	1167 t	7.7	1256	7.9
Night	4	1137 t	19.8	1402	19.3
Day+ Night	8	1152 t	13.9	1329	15.4
		CV% range		CV% range	
Within transects					
Day	4	19.8–117.8		19.0–128.5	
Night	3–4	14.9–73.0		14.3–64.1	
Day+ Night	7–8	16.6–65.8		31.4–68.1	
Among transects					
Day	4	54.3–106.7		58.4–100.6	
Night	4	24.5–67.3		20.6–62.2	

Aglen (1983) derived an empirical formula for predicting the CV based on the ratio of linear distance surveyed (L) over the square root of the surveyed area (A), which he called the "degree of coverage" or DOC:

$$Predicted\ CV = 0.5\left(\frac{L}{\sqrt{A}}\right)^{-0.41}.$$

The variance among the eight series replicates of the area were significantly less than the predicted value from Aglen's formula whereas the variance for the combined area of B5 and B6 was higher (Table 8). In both cases, the observed variance among surveys was typical of acoustic surveys.

Discussion

We have assumed that the dominant part of the acoustic signal selected from the short transects represented yellowtail rockfish, a conclusion supported by fishing results and the continuity on the echograms between diurnal and nocturnal distribution. The longer sections of the transects, which indicated about 16% (5–30%) more total biomass, probably included other species of deeper-dwelling rockfishes.

Yellowtail rockfish share with other species a diel pattern of diurnal schooling and nocturnal dispersal (Simmonds et al., 1992). We observed that the schools reform at dawn near a minor but nearly continuous topographic feature that crosses the study area on a north–south axis. The strong and persistent affiliation of yellowtail rockfish with this small cliff is consistent with long-term commercial fishing records at this location. The diurnal schools are near the bottom at dawn then rise slowly during the day, dispersing at dusk. This is congruent with fishermen's observations that early morning is the most productive time for bottom trawling for this species. The fidelity to topographic features is consistent with reports of Pearcy (1992) and Carlson and Haight (1972). Pearcy's reports on acoustically tagged specimens includes an example of "homing" near to the original capture sites, even as far as 2 nmi overnight.

Because we conducted the study at only one time of year, we could not examine how diel behavior would vary with season. Fishermen report that yellowtail rockfish occupy the "cliffs" at all times of year. They also report that the dawn tows are the best fishing on a year-round basis. We would suggest that if diel vertical movement is triggered by or at least associated with light intensity at depth, then the effect would be more obvious during summer months when light intensity increases and the twilight period shortens. It might also be more dramatic on brighter days.

The diversity of species, especially near the shelf edge, illustrates that a difficult issue facing acoustic assessment of rockfish will be species identification. This process will be complicated by the difficulty of trawling much of the habitat. Our study was based on single-beam and single-frequency acoustic observations. Encouraging results on species identification have been obtained by more advanced acoustic analysis of individual fish schools (Kieser and Langford, 1991; Scalabrin and Masse, 1993), comparison of day and night survey data (Gerlotto, 1993), and multifrequency and wide band observations (Simmonds and Armstrong, 1990; Zakharia, 1990). In this context, innovative transducer design and deployment will be important to obtain more detailed acoustic data from individual fish and schools near the bottom.[2] Supplemental information on habitat and depth preference by species, perhaps developed from simultaneous use of submersible devices or side-scan bathymetry, may help to estimate species' proportions (Richards et al., 1991).

Diurnal versus nocturnal density and biomass estimates

Although the echograms showed differences in diel distribution for yellowtail rockfish, they did not indicate the extreme densities which lead to acoustic shadowing (Foote, 1990). In contrast to other studies (summarized in Appenzeller and Leggett, 1992), which report higher density estimates from night observations, our day and night estimates were similar. We conclude that, for yellowtail rockfish, diel behavior patterns do not bias hydroacoustic biomass estimates. It remains possible, however, that the similarity between diel periods is purely fortuitous in that the various factors that could affect estimation, such as movement in and out of the study area

Table 8

Observed coefficient of variation (CV) of biomass estimates from short section in comparison with predicted CV from formula by Aglen (1983). Sample size, *n*, is the number of replicate coverages of either the area represented by transects B5 and B6, or the overall area of B2–B9.

Transect	*n*	Section	Distance (km)	Area (km²)	DOC	Predicted CV%	Observed CV%	Mean estimated biomass (t)
B5-6	19	Short	11.0	15.2	2.82	32.7	48.0	397
B2-9	8	Short	39.6	55.5	5.33	25.2	13.9	1152

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[2] Dalen, J., and H. Bodholt. 1991. Deep towed vehicle for fish abundance estimation, concept and testing. ICES Council Meeting (CM) 1991/B:53, 13 p. [Mimeo.]

or diel variability in tilt angle, may simply have cancelled each other out.

We assumed that there are no diel changes in fish target strength. Such changes have been observed for other species and have been linked to swimming behavior or mean tilt angle (Miyashita et al., 1995; Buerkle and Sreedharan, 1981; Olsen, 1990; Misund, 1997). Target strength variation between night and day may be smaller for yellowtail rockfish because these fish tend to remain in the same general depths. They are not moving from the bottom to surface waters and therefore not encountering large relative changes in pressure.

The observed diel behavior of increased aggregation during the day led us to hypothesize that variance in biomass should be greater for diurnal observations. We observed that yellowtail rockfish move towards the cliffs at dawn. We assumed that they would concentrate further along that narrow band to produce discrete schools. We viewed the nocturnal distribution as a relatively dispersed band (three-dimensional cloud) of individuals in the general vicinity of the cliffs. We assumed that the diurnal distribution, which lay along the orientation of the cliff, would be a much narrower string of individual schools and hence of highly varying density, perhaps to the extent of approximating a "beaded pattern" of distinct schools following the length of the cliff. We expected that diurnal estimates derived from transects that pass perpendicular to the cliffs would be highly variable because the path of the acoustic beam could range from "missing entirely" to "completely ensonifying" a dense school.

We found that, for the short transect version of the all-transect data, the variance of diurnal biomass estimates was not significantly greater than that of nocturnal biomass estimates. Diurnal variance was significantly higher in the expanded set of the B5–B6 set of observations but only for the long version of transect B6.

The weak or mixed indication of higher diurnal variance implies that the apparent aggregation towards the cliffs, evident in the echograms, is not matched to the same degree by aggregation along the axis of the cliffs. We expected discrete diurnal schools following the axis of the cliffs. This tendency to aggregate into a continuous band of fish along the cliffs, as opposed to discrete schools, may be unique to this area where there is a longitudinal topographic feature along the preferred depth. In areas of the coast lacking in such a linear feature, fish may tend to aggregate over a specific point, such as a pinnacle, producing greater daytime variance among estimates of biomass. Results of this experiment, however, do not support the hypothesis that estimates from the dispersed condition will show less variance for yellowtail rockfish. The similarity in variance between nocturnal and diurnal periods indicates that no substantial gains in efficiency or precision can be achieved by sampling during one or other of the diel periods.

The among-transect variance overwhelms the other sources of variance even within a small coastal area. From the perspective of two-stage sampling (among-transect or within-transect variance), precision of the overall estimator is reduced by allocating sampling effort in proportion to variance contributed by each stage. Because among-transect variance is much greater, survey design should maximize the number of transects at the expense of replicating transects. The only exception to this principle would arise when the cost of replicate samples is much lower. Because the cost of collecting a replicate transect estimate is almost equal to that for an additional transect over the scale we are considering, it would be more efficient to maximize the number of different transects.

By repeating the survey eight times, we were able to determine the variance of the biomass estimate directly rather than by inferring it indirectly through geospatial analysis of "within" variance (Petitgas, 1993). This calculation of "among" survey variance follows from work by Williamson (1982), who resampled from the individual samples averaged over one minute within a transect, and by Robotham and Castillo (1987), who bootstrapped cumulative transect observations as we did. There is no question that a formal investigation of the spatial impact on variance would require treatment at the granular level of the observations, which the geospatial methods provide. These procedures also facilitate an investigation of the impact of additional explanatory variables and development of model-based inference. However, the requirements of our study were realized by the simpler transect-based analysis.

Total biomass estimate and survey design

The overall biomass estimate of 1152 t for the study area appears consistent with overall coastal biomass estimates of 50,000–60,000 t for a stock that is assumed to extend from the study area to the border of B.C. and Alaska (Stanley, 1993). The fact that the overall coefficient of variation among the eight series for the study area was under 14% is encouraging and better than that predicted from the formula of Aglen (1983). This precision may not, however, apply to all rockfish species. Wilkins (1986) found that the CV for widow rockfish was 2–3 times higher in spite of a more comprehensive estimation procedure that included the use of side-scan sonar in conjunction with echosounding. We can also expect greater variation if repeated estimates were conducted at greater time intervals.

Over a one-week period and an area of over 100 km^2, we have demonstrated precision (CV=15%) in acoustic biomass estimates that is acceptable in a stock assessment context for yellowtail rockfish. Variance among replicated transects is low enough that survey effort can be distributed to maximize the number of different transects, either to increase the area of the survey or the density of coverage. We have shown that a survey of yellowtail rockfish can be conducted throughout the diel cycle and thus reduce survey costs.

This study also indicates that yellowtail rockfish can aggregate within a well-defined bathymetric range near topographic features. If these tendencies are consistent over the whole range of this species, they may provide the basis for stratification and possible further gains in efficiency. Our results indicate that a simple systematic transect design with transects oriented perpendicular to the long axis of the fish concentrations (the edge of the continental shelf) is a satisfactory choice for the elementary sampling distance unit (ESDU) (Simmonds et al., 1992; Simmonds and Fryer, 1996). If the preferable depth range is narrow over most of the coastline and the survey must thus cover a long narrow corridor, then a systematic zig-zag would be preferable (Simmonds et al., 1992).

The affiliation of yellowtail rockfish with a minor topographic feature within a depth range indicates that the density distribution of yellowtail rockfish is "nonstationary," in that the densities will not be randomly distributed in a study area or stratum, even after bathymetric stratification (Simmonds et al., 1992). This is an important characteristic of the species and should be noted if more advanced survey design and analysis procedures, such as geostatistical spatial averaging and cokriging, are to be investigated (Foote and Stefansson, 1993; Marcotte, 1991).

Although the results of the experiment support the potential for acoustic estimation of this species, the generality of the conclusions will have to be tested over a larger scale and more varied habitat. The study site was chosen carefully to minimize the unknowns, in particular the presence of other species. The hypotheses will have to be re-examined over different depths and topography. It is also possible that the annual cycle of maturation, mating, and parturition for these live-bearing fish may be associated with different behavior.

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Variability in reactions of Pacific harbor seals, *Phoca vitulina richardsi*, to disturbance

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Abstract.–Disturbances to harbor seals, *Phoca vitulina richardsi*, during 1991 and 1992 pupping seasons were observed at Puffin Island, Clements Reef, and Skipjack Island in Washington state. Harassment ($\geq$ one seal entering the water) of seals ashore was common ($\geq$71% of survey days) and primarily caused by powerboat operators approaching to observe seals. Recovery (number of seals on a haul-out site returned to preharassment levels) following a harassment was less at Puffin Island (19%) than at Clements Reef (54%) and Skipjack Island (45%). Additionally, seals were more vigilant ($P<0.003$) at Puffin Island than at the other two locations. These results indicated that seals at Puffin Island were less tolerant of disturbance than seals at other sites. This could possibly be attributed to a greater ($P<0.05$) percentage of pups ashore (17%) than at Clements Reef (3%) and Skipjack Island (3%). Because of this, we expected that powerboats would disturb seals from greater distances at Puffin Island. To test this, we used a theodolite to determine distance between seals and an approaching vessel at Puffin Island and Clements Reef. There was, however, no significant ($P>0.05$) difference in distances at which disturbances occurred. The most notable difference in distance of disturbance was between initial and subsequent harassments during a haul-out period. Those seals remaining or returning to shore after a harassment were more tolerant of powerboats, allowing significantly ($P<0.05$) closer approaches than those initially harassed. Seals detected (head raised and oriented toward the potential disturbance) a powerboat at a mean distance of 264 m, and harassments occurred when boats approached, on average, to within 144 m. Results of this study exemplify the variability in reaction to disturbance and the necessity for considering these differences for minimizing disturbance.

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In many locations, disturbance is an important factor affecting the haul-out patterns of harbor seals, *Phoca vitulina*. Disturbance is defined as any activity that alters normal behavior. In the United States, disturbance of marine mammals by humans is regulated by the Marine Mammal Protection Act of 1972. In contrast to pelagic marine mammals, changes in the behavior of pinnipeds on haul-out sites related to disturbance is relatively simple to measure. Long-term effects of disturbance, however, are often difficult to assess.

The effects of disturbance may be quite mild or may cause displacement and even mortality. Bighorn sheep (*Ovis canadensis*) and white-tailed deer exposed to snowmobile traffic have shown increased heart rate but no visible change in behavior (MacArthur et al., 1982; Moen et al., 1982). Humpback whale (*Megaptera novaeangliae*) female-calf pairs in Hawaii have avoided nearshore areas of intense human recreational activities (Salden, 1988; Glockner-Ferrari and Ferrari[1]). Disturbance-related mortality in harbor seals can result from stampeding and pup abandonment (Johnson[2]). Disturbance from low-flying aircraft may have caused mortality of more than 200 (10%) harbor seal pups on Tugidak Island, Alaska, in 1976 (Johnson[2]).

In addition to aircraft, sources of disturbance include boats, seismic exploration, pedestrians, kayakers, and natural predators (Renouf et al., 1981; Laursen, 1982; Allen et al., 1984; Terhune, 1985; Richardson et al., 1995; Moss, 1992; Kroll, 1993; Johnson[2]; Murphy and Hoover[3]; Calambokidis et al.[4]; and others). Allen et al. (1984) reported that harbor seals on a haul-out site in Bolinas Lagoon, California were disturbed by humans on 71% of survey days; most disturbances were caused by nonmotorized boats (primarily canoes). Humans, primarily boat operators, were the most common cause of harassment to harbor seals on Protection Island (Kroll, 1993) and Woodard Bay (Calambokidis et al.[4]), Washington. Sources of disturbance to harbor seals ashore at Gertrude Island, Washington, were mainly unidentifiable; however, of detectable causes, human activities and coyotes were the most common (Moss, 1992).

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Reaction to disturbance may vary among harbor seal groups within an area (Terhune and Almon, 1983) and according to disturbance sources (e.g. powerboats vs. canoes and kayaks; Calambokidis et al.[4]). This variability may be attributed to different levels of tolerance among age, sex, or reproductive status of harbor seals. Reaction to different causes of disturbance may vary with exposure to particular sources, eventually resulting in greater avoidance or tolerance. In any case, results of previous studies indicate that reaction to disturbances vary within and among regions, although little quantitative evidence exists.

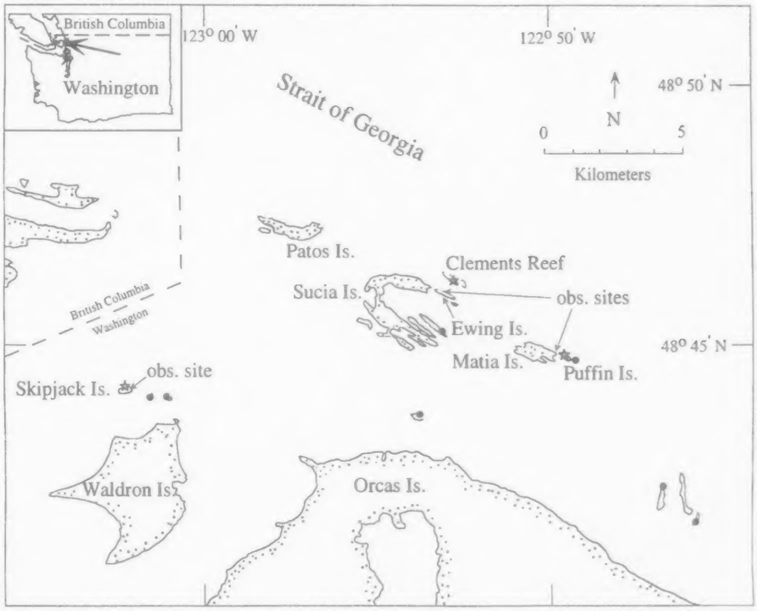

Figure 1

Locations (★) of harbor seal haul-out sites observed at Clements Reef, Puffin Island, and Skipjack Island during 1991 and 1992 pupping seasons in the San Juan Islands, Washington. Dots (●) indicate other haul-out sites in the area.

In this study, we collected data to evaluate the extent of disturbance to harbor seals at haul-out sites in the northern San Juan Islands. Our objectives were to determine 1) if human-related activities were the primary source of disturbance; 2) if recovery varied between flood and ebb tides and was similar among the three haul-out sites (one location was a pupping area); 3) if vigilance characteristics differed among haul-out sites; 4) if the response to harassment was similar for pups and for adults and subadults; and 5) if the mean distance between harbor seals and a boat causing a disturbance varied within and among haul-out sites and, if so, to determine potential causes of this variability.

Methods

Study area

The study area was located in the northern San Juan Islands, Washington (Fig. 1). This area is characterized by numerous islands, a tidal range of 3.6 m, strong currents (maximum of 7.7 km/h), and a rocky shoreline. Haul-out sites of harbor seals, which include reefs and rocky intertidal zones of islands, are numerous but typically are used by fewer than 100 animals. During this study, observations were conducted at Clements Reef, Puffin Island, and Skipjack Island (Fig. 1).

Observations of haul-out sites

Ground-based surveys of harbor seals were conducted at Clements Reef (n=13), Puffin Island (n=9), and Skipjack Island (n=8) from 2 July to 19 August 1991. In 1992, surveys were conducted between 24 June and 10 September 1992 at Clements Reef (n=21) and Puffin Island (n=18). Skipjack Island was not surveyed during 1992 to allow increased sampling effort at the other two sites. Seals at each location were observed at least twice a week (one observer per site). Seals at Clements Reef were viewed from Ewing Island (Fig. 1), approximately 0.55 km away. Seals on the northwest end of Puffin Island were viewed from the southeast corner of Matia Island, 0.38 km away (Fig. 1). Observer heights above zero tide level were 10 m at Clements Reef and 13 m at Matia Island. The observation point on the northeast side of Skipjack Island was directly above (23 m) the haul-out site (Fig. 1).

Observations of harbor seals began one to three hours before low tide and ended three to seven hours after low tide (when <50% of the maximum number of seals counted during that tide cycle remained ashore).

Seals were viewed with 22× and 15–60× spotting scopes. Scan surveys (Altmann, 1974) were conducted at ten minute intervals throughout the observation period. During each half-hour period, the first scan was a count of all seals, the second scan included size structure (number of harbor seal pups and subadults and adults), and the third scan was used to quantify vigilance of seals (head up, alert but not oriented toward a disturbance source) and sources of disturbance (within 1.0 km of the haul-out site). Counts of size structure included only those individuals that could be assigned a given category (e.g. seals were not included if only a flipper was visible as in the first scan).

Counts from these scans were used to determine how many seals entered the water following a disturbance and when recovery had occurred. Recovery was measured by the increase in number of harbor seals on the haul-out site after harassment. Recovery was divided into four categories: 1) full recovery (number of seals ashore after harassment returned to preharassment levels); 2) partial recovery (number of seals ashore increased after the harassment, but did not reach preharassment levels); 3) no recovery (number of seals ashore did not increase after harassment); and 4) no chance to recover (number of seals ashore never increased after harassment owing to repeated disturbances or rising tide washing over the haul-out site). Because animals were not marked, full recovery did not imply that individuals returning to shore were necessarily the same ones that were harassed, but partial and no recovery did indicate certain individuals did not return to the haul-out site.

Terhune (1985) and da Silva and Terhune (1988) reported that the number of vigilant harbor seals was dependent on group size. To eliminate the potential effect of group size on vigilance, the original data were subsampled to produce subsets of equal group sizes. Therefore, a single value is not presented for a site because it varies with each comparison.

Data were collected for every potential source of disturbance that approached the haul-out site. Sources were divided into the following categories; airplanes, powerboats (including sailboats under motor power), sailboats, kayaks and canoes, people, bald eagles (*Haliaeetus leucocephalus*), unknown, or other. Vessel speed was classified as underway fast (creating a breaking bow wake), underway slow (nonbreaking bow wake), and drifting (motor not in gear or turned off). Harbor seal reactions to a disturbance were categorized as 1) detection: ≥1 seal with head raised and oriented toward potential disturbance source; 2) alarmed: ≥1 seal moved from its resting place, but did not enter the water; and 3) harassed: ≥1 seal entered the water.

Positions of an approaching vessel were monitored by using a Nikon NT2A or Pentax TH20D theodolite. Bearings to the approaching vessel and seals exhibiting disturbance reactions were recorded. The distance from theodolite to vessel or seal was calculated by using the tangent of the vertical angle from the theodolite and height of the theodolite above the water. The distance between vessel and seals was calculated by using the Law of Cosines that incorporates distances between theodolite and vessel and theodolite and seals and by using the horizontal angle between the vessel and seals (from theodolite). Height of the theodolite above water was measured directly or estimated from a cosine prediction of tide height (San Juan Current and Tide Tables, published by Island Canoe, Bainbridge Island, Washington). The tidal constituent used was Port Townsend, Washington, with a correction for Echo Bay, Sucia Island (approximately 1 km from Ewing Island and 6 km from Puffin Island). The observation point at Ewing Island (for Clements Reef surveys) was near a vertical rock ledge, which allowed the observer to measure theodolite heights above water level (using a tape measure with float attached). Direct measurement of height above water was accurate to approximately 0.1 m. Direct measurement was not possible at Puffin Island; therefore, theodolite heights above water level were based on tide height predictions, which were accurate to approximately ±0.3 m. Error in theodolite locations was less than 10 m; accuracy was based on calibration with fixed objects (e.g. buoy or island).

Analyses

Results of statistical analyses were considered significant at $\alpha = 0.05$. Mean percentage of pups among the sites was compared by using analysis of variance (ANOVA) with arcsine transformation. A Tukey multiple comparison test was used for significant ANOVA results (Zar, 1984; Day and Quinn, 1989). To test whether pups were less tolerant of disturbance than adults, the frequency of positive and negative changes in the proportion of pups ashore before and after a harassment was compared by using a chi-square goodness-of-fit test (data were combined from all sites). Percentage of vigilant seals was compared between sites by using Mann-Whitney U tests (separate two-sample tests were conducted owing to random subsampling to control for group size). Differences in distance of disturbance among powerboat approach speeds were tested with Mann-Whitney, t, and Kruskal-Wallis tests. Significant differences in distance of disturbance among categories of detection, alarm, and harassment were detected with

Table 1

Summary of numbers of harbor seals using haul-out sites and primary disturbances occurring during the pupping season of 1991 and 1992 in the northern San Juan Islands, Washington.

	Puffin Island	Clements Reef	Skipjack Island
No. of seals (range)	50–125	125–275	50–125
% pups (SE)	17% (1.1)	3% (0.3)	3% (0.4)
% of days with harassment (n)	77% (27)	71% (34)	88% (8)
No. of harassments observed	64	91	24
% of harassments caused by powerboats	42%	76%	46%
Unknown[1]	19%	2%	38%
Bald eagle	16%	2%	0%

[1] No disturbance source was detectable by the observer.

ANOVA with square root transformation. Initial versus subsequent disturbances were compared within each disturbance categories with t-tests. Randomization statistics (Resampling Stats, Inc., 1995) were used in calculation of power to detect significant differences.

Results

Clements Reef was the largest haul-out site with the greatest number of seals. Puffin Island, however, had the greatest number of pups, the pups representing a significantly (F=97.6, P<0.01) greater percentage of the total number of seals ashore in comparison with Clements Reef (Table 1). The study area on Puffin Island appeared to be an important area for female-and-pup pairs and thus may explain some of the observed differences in reactions to disturbance.

Harassments of seals occurred during at least 71% of the survey days. The primary cause of disturbance was powerboats (Table 1). Most of these (74%, n=96) involved boat operators approaching haul-out sites to view seals. The second most common category of disturbance was unknown (no source was visible or audible to the observer) and was most prevalent at Skipjack Island. Bald eagles were the third most common cause of disturbance and were more frequent at Puffin Island than at other sites. In contrast with powerboats, sea kayaks were uncommon during the study and, therefore, caused fewer harassments (11% for all sites). Sea kayakers, however, were a greater potential disturbance to seals ashore than operators of powerboats. Fifty-five percent of kayakers (n=11) within 1 km of a haul-out site harassed harbor seals, whereas only 9% of powerboats (n=436) within 1 km caused harassment. This finding is a result of seals being less tolerant of kayaks and kayakers who generally travel closer to shore than do powerboaters.

Table 2

Percentage of harassments (n, excluding disturbances caused by bald eagles) that resulted in either full recovery, partial recovery, no recovery, or no chance to recover for harbor seals at Puffin Island, Clements Reef, and Skipjack Island, northern San Juan Islands, Washington, 1991 and 1992.

	Puffin Island (n=27)	Clements Reef (n=28)	Skipjack Island (n=11)
Full recovery	19%	54%	45%
Partial recovery	30%	32%	18%
No recovery	44%	7%	36%
No chance to recover	7%	7%	0
For all recoveries			
no. of harassments before low tide	10	11	5
no. of harrassments after low tide	17	17	6

The extent of recovery following harassments (excluding those caused by eagles) of harbor seals was less at Puffin Island than at Clements Reef and Skipjack Island (Table 2). Disturbances caused by eagles were excluded from this comparison because eagles were potential predators of pups (eagles were observed approaching and disturbing pups) and could affect recovery. Recovery was related to whether the harassment occurred before or after low tide (74% of full recoveries occurred before low tide, whereas 75% of partial and 89% of no recoveries occurred after low tide). This finding corresponds with total numbers of seals ashore typically decreasing one to two hours after low tide, independent of disturbance. For comparison of recovery among sites, the proportion of disturbances occurring before and after low tide was similar and likely did not influence results (Table 2).

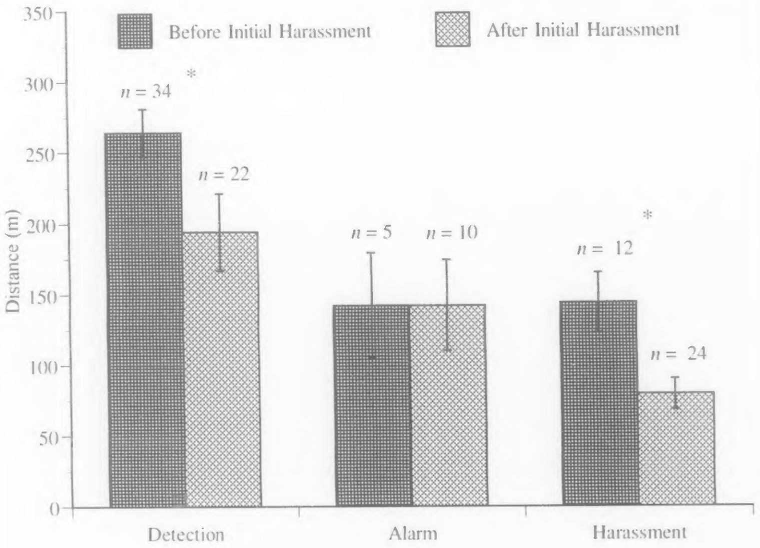

Figure 2

Mean distance (±SE) between harbor seals and powerboat for disturbances occurring before and after the initial harassment during a haul-out period. An asterisk (*) indicates a significant ($P<0.05$) difference between before and after initial harassment data for that disturbance category.

There was no apparent difference in the proportion of harbor seal pups onshore before and after harassments ($\chi^2=0.183$, $n=27$, $P>0.50$). Pups did not appear to be affected disproportionately to subadults and adults.

The percentage of vigilant harbor seals varied with each comparison (due to random subsampling of data to control for group size), hence there was no single value for percentage of vigilant harbor seals at each haul-out site. The percentage of vigilant harbor seals was significantly greater at Puffin Island compared with Clements Reef ($P=0.003$) and Skipjack Island ($P=0.002$; Table 3). This finding is likely due to the greater percentage of female-and-pup pairs at Puffin Island and, in addition to lower recovery, indicated seals were more susceptible to disturbance.

Powerboat speed did not significantly influence distance of disturbance. Lack of statistical significance was likely due to small sample sizes after subdividing data by approach speed and initial versus subsequent harassments. There was also no significant difference in distance of disturbance between sites (data were not collected at Skipjack Island). Given the large variability of the data and small effect size, greater than 450 observations would be required for a power of 0.80 to detect a significant difference between sites. Data, therefore, were pooled for further analysis. Twenty-five percent of harassments occurred when vessels were <100 m from seals, 50% occurred at 100–200 m, and 25% at 200–300 m. After detection by seals, powerboats were able to approach significantly closer ($F=10.51$, $P<0.001$) before causing alarm or harassment of seals (Fig. 2). Interestingly, we found that distances of initial disturbance were significantly greater than subsequent disturbances (Fig. 2). This indicated that seals remaining or returning to shore following the first harassment were less easily disturbed.

Discussion

Many islands in the San Juan Archipelago are state parks or have resort harbors that attract numerous boaters during the summer. Clements Reef is located near (0.6 km) Sucia Island, which is the most heavily visited state park in the northern islands. It was not surprising, therefore, that most disturbances at Clements Reef were caused by boaters. Relatively few kayakers ventured out to Clements Reef, Puffin Island, or Skipjack Island. Kayakers typically travel along the shoreline and have been shown to cause

Table 3

Mean percentage of vigilant harbor seals at Puffin Island versus Clements Reef and at Puffin Island versus Skipjack Island when no potential disturbance source was within 1 km of haul-out site. Two means (±SE) and separate statistical tests are presented for Puffin Island due to random subsampling to control for group size of each comparison.

	Mean (%)	SE	*n*	Mann-Whitney *U*	*P*
Puffin Island	4.43	0.44	17		
Clements Reef	2.41	0.47	17	U=229	0.003
Puffin Island	6.40	1.13	21		
Slipjack Island	2.46	0.75	21	U=343	0.002

harassment of harbor seals at a greater distance than do operators of powerboats (Calambokidis et al.[4]); therefore, as sea kayaking becomes more popular, there is a greater potential for disturbance of harbor seals ashore.

The differences in occurrence of unknown causes of disturbance among haul-out sites was possibly a result of haul-out site topography. Harbor seals on Clements Reef had a 360° view of potential sources of disturbance compared with roughly a 270° view for Puffin Island and 180° for Skipjack Island. A disturbance of unknown origin at Skipjack Island would often begin by several harbor seals looking toward the rocky cliff of the island, then entering the water. A high incidence of disturbances of unknown origin have also been documented at Gertrude Island (77%; Moss, 1992) and Protection Island (43%; Kroll, 1993), Washington. The relatively high occurrence of harassments by bald eagles at Puffin Island may have been due to a nearby bald eagle nest and the high percentage of harbor seal pups (immature eagles were observed harassing female and pup pairs). Skipjack Island also had an active bald eagle nest, but eagles were not observed harassing harbor seals.

Overall, only 39% of all harassments resulted in full recovery, indicating seals often remained in the water or moved to a different site. Allen et al. (1984) reported that the number of harbor seals that returned to a haul-out site after a disturbance in Bolinas Lagoon, California, was always less than the original number, and in most cases, harbor seals did not move to a nearby reef. Murphy and Hoover[3] reported that harbor seals off the Kenai fjords, Alaska, often searched for a new haul-out site after harassment. Disturbance to harbor seals, therefore, may have considerable impact where haul-out space is limited (Murphy and Hoover[3]). Although haul-out sites in the San Juan Islands are numerous, alternate sites for female and pup pairs, similar to Puffin Island, may not be readily accessible (particularly since there tended to be less recovery of seals at Puffin Island).

Terhune (1985) compared aggregation behavior and vigilance of harbor seals with flocking behavior of avian species—a behavior that allows individuals to decrease their surveillance without decreasing the probability of detecting a predator (Caraco, 1979; Studd et al., 1983). Da Silva and Terhune (1988) identified group size as the only factor accounting for variation in time taken to scan for predators. Renouf and Lawson (1986) suggested that only males increased scanning time as mating season approached, and scans were related to important events in their mating system, not predators. Results of our study indicated that increased vigilance may be related more to potential "predators" (loosely defined as any source of disturbance, human or animal). We found that seals at an area with a greater percentage of female-and-pup pairs scanned more frequently than those at other locations. Other researchers have described increased vigilance of females with pups. Stein (1989) reported female harbor seals rested alert significantly more frequently when their pups were one to nine days old than when pups were older. Newby (1973) reported a female harbor seal with a pup is "constantly alert and nervous."

The greater vigilance of harbor seals at Puffin Island than at Clements Reef and Skipjack Island and the lack of recovery from a harassment indicated that seals at a pupping location were affected more by disturbance. We therefore expected that seals at Puffin Island would enter the water when powerboats were farther away, in contrast with harbor seals at Clements Reef. This was not the case, there were no significant differences between sites. We cannot, however, conclude that seals at pupping locations tolerated boats to approach just as closely as seals at nonpupping sites without harassment because of differences in geographic characteristics of haul-out sites, unreplicated sites, and lack of power to detect a statistically significant difference.

Bishop (1967) observed that a nucleus of harbor seals, which usually included several very large animals, remained ashore unless danger became imminent. Although we also observed certain groups of harbor seals (often small-size groups) entering the water well before others during a harassment, there was no significant trend. Terhune and Almon (1983) also noted that not all groups of harbor seals reacted to disturbances in the same manner.

The most notable difference in distance of disturbance was the decrease between initial and subsequent harassments. There are two plausible explanations for this: 1) seals became more tolerant of powerboat approaches; or 2) seals that were less tolerant of disturbance did not return to the haul-out site after the initial harassment. Based on lack of full recovery following initial harassments, our results support the latter possibility.

Allen et al. (1984) reported that boats advancing toward, or remaining near, harbor seals ashore at Bolinas Lagoon, California, caused seals to leave the haul-out site more often than a boat simply moving past seals. Boats that traveled slowly, parallel to the haul-out site, and made no abrupt move or changes in speed approached harbor seals at Clements Reef and Puffin Island with minimal disturbance. Greater sample sizes probably would have resulted in significant differences among distances of disturbance for various approach speeds and angles recorded during this study.

Additional potential factors affecting the distance at which seals were disturbed included time of day for haul-out period or location of haul-out site. Harbor seals may more readily enter the water toward the end of the haul-out period, if air temperature is high (Watts, 1992), or during rain. These considerations were not addressed in this study. Harbor seals also may become accustomed to close approaches (<15 m) by boats in areas of high boat traffic (authors' pers. obs.). In Woodard Bay, Calambokidis et al.[4] reported powerboats were able to approach to an average of 40 m before harbor seals entered the water. This area near Seattle, Washington, undoubtedly gets more year-around recreational traffic than the northern San Juan Islands which may explain why disturbance distances were over a third less than those observed during our study.

Most harassments in our study were caused by people approaching to view harbor seals. It is important therefore to distribute information and guidelines for wildlife viewing to the general public. An effective solution may be to include information with vessel registration.

Direct mortality of harbor seals or long-term abandonment of haul-out sites (greater than one haul-out period) because of harassment by humans was not observed during this study. Long-term impacts of harassment of harbor seal populations, however, are difficult to assess. Cases where marine mammals remain in heavily disturbed areas are easy to detect; therefore, cases of partial or complete abandonment of disturbed areas may be more common than evidence indicates (Richardson et al., 1995). Harassments increase energy expenditure of harbor seals by decreasing duration of haul-out period. Increased energy requirements likely have the greatest impact on harbor seal pups during nursing and on adult and subadult harbor seals during molt when access to haul-out sites is important. Brasseur et al. (1996), however, demonstrated that captive harbor seals may need to haul-out even outside these "critical" periods. Richardson et al. (1995) noted that occasional disturbance probably has little effect on harbor seal populations; repeated disturbance, however, may have significant negative effects especially at haul-out sites used for pup rearing.

Results of this study quantify the variability in response to disturbance among individuals and locations. We also demonstrated the potential bias in sampling animals that remain after an initial disturbance, or in areas of regular boat traffic. Distance at which powerboats caused harassment were variable, ranging from 28 m to 260 m. Boating regulations near harbor seal haul-out sites should address activity of vessel (speed and approach angle) in addition to distance from harbor seals. Boating precautions are particularly important near harbor seal pupping areas such as Puffin Island.

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Abstract.–Age structure, longevity, and mortality were determined for a population of blackcheek tonguefish, *Symphurus plagiusa*, in Chesapeake Bay. Blackcheek tonguefish (36–202 mm TL) were randomly collected by means of otter trawl in lower Chesapeake Bay and major Virginia tributaries (James, York, and Rappahannock rivers) from April 1994 through August 1995. Ages were determined by interpreting growth increments on thin transverse sections of sagittal otoliths. Marginal increment analysis showed that a single annulus was formed in June of each year. Blackcheek tonguefish caught during this study reached a maximum age of 5+ years. Growth was rapid during the first year, then slowed rapidly at a time coincident with maturation. We used the following von Bertalanffy growth equations: for males—$L_t = 196.5(1 - e^{-0.285(t + 0.92)})$; and for females—$L_t = 190.6(1 - e^{-0.320(t + 0.78)})$. Von Bertalanffy parameters were not significantly different between sexes. Extrapolated instantaneous mortality rates for a possible seventh year class were 0.73 (Hoenig's equation) and 0.77 (Royce's equation). High estimates of instantaneous total mortality may reflect either loss due to emigration of adults from Chesapeake Bay onto the continental shelf or high natural mortality occurring in this northernmost population. Compared with sympatric pleuronectiforms, blackcheek tonguefish have a relatively high mortality rate, small asymptotic length, and high growth parameter *K*. Species, such as blackcheek tonguefish, that feature this combination of growth parameters are hypothesized to be better adapted at exploiting seasonally dynamic and highly unpredictable environments, such as those estuarine habitats within Chesapeake Bay.

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Age, growth, longevity, and mortality of blackcheek tonguefish, *Symphurus plagiusa* (Cynoglossidae: Pleuronectiformes), in Chesapeake Bay, Virginia*

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The blackcheek tonguefish, *Symphurus plagiusa* (Linnaeus, 1766), ranges from Connecticut southward through the Florida Keys, northern Gulf of Mexico, Cuba, and the Bahamas (Ginsburg, 1951; Topp and Hoff, 1972; Munroe, 1998). Chesapeake Bay is the northernmost location of a major population of this species (Munroe, 1998). South of Chesapeake Bay, blackcheek tonguefishes are an abundant component of the fish fauna occurring in estuaries and inshore coastal waters. Within this region, they occur in sufficient numbers to form a minor component of the bycatch of demersal fisheries and also constitute a minor inclusion in landings reported for several industrial fisheries. In the shrimp trawl fishery, they are a potential nuisance because individuals frequently become embedded in the webbing of trawls to such an extent that they interfere with the gear's effectiveness (Topp and Hoff, 1972).

The blackcheek tonguefish is the only member of the pleuronectiform family Cynoglossidae occurring in Chesapeake Bay (Ginsburg, 1951; Murdy et al., 1997; Munroe, 1998). This species is among the top three most abundant pleuronectiforms occurring throughout lower Chesapeake Bay and its tributaries (Bonzek et al., 1993; Geer et al., 1997). Only the hogchoker, *Trinectes maculatus*, is commonly taken in greater abundance in bottom trawls made within the Bay. Occurrence of all life history stages in Chesapeake Bay (Olney and Grant, 1976; Terwilliger, 1996) suggests that blackcheek tonguefish is a resident species in this system.

Despite its abundance in different estuarine and nearshore marine habitats in the northwest Atlantic, life history parameters of *S. plagiusa* are largely unknown. Some previous works have described distribution, relative abundances and length frequencies for blackcheek tonguefish in South Carolina estuaries (Shealy et al., 1974); some have summarized size-related maturity patterns for individuals from throughout the entire range of the species (Munroe, 1998); some have investigated factors influencing recruitment (Miller et al., 1991); and some have described daily growth rates of juveniles in Georgia estuaries (Reichert and van der Veer, 1991). The minimal amount of published information on this species (summarized in Munroe, 1998) may be due in part to the relatively small size of the fish. It reaches a maximum size of approximately 210 mm total length (TL) (Wenner and Sedberry, 1989), but fish smaller than 165 mm TL are those most commonly taken in Chesapeake Bay by otter trawl (Terwilliger, 1996; Geer et al., 1997). Small size and benthic microinvertebrate feeding habits (Stickney, 1976; Reichert and van der Veer, 1991; Toepfer and Fleeger, 1995) render this species inaccessible to most recreational and commercial fishing gears used in Chesapeake Bay.

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Few age and growth studies using bony structures or otoliths exist for species of the Cynoglossidae. This relatively large gap in knowledge for approximately 150 species of tonguefishes was recently noted in a compilation of flatfish life history parameters (Miller et al., 1991). Although several studies have described growth for species of *Cynoglossus* from the eastern Atlantic (Chauvet, 1972), western Pacific (Lin, 1982; Meng and Ren, 1988; Zhu and Ma, 1992), and Indian Ocean (Seshappa, 1976, 1978, 1981; Ramanathan et al., 1980; Seshappa and Chakrapani, 1984), no growth studies using bony structures or otoliths have been performed on species of *Symphurus*. Previous work describing the age structure of blackcheek tonguefish in Chesapeake Bay using length frequencies of fish taken by otter trawl (Bonzek et al., 1993) is limited because this type of analysis requires subjective interpretation of modal frequencies in the data, which, given the difficulty of distinguishing modal groups at older ages, renders the interpretation unreliable (Chauvet, 1972; White and Chittenden, 1977; Jearld, 1983; Barbieri, 1993). Such limitations in interpretation of age from length-frequency distributions are particularly evident in data from Koski's (1978) study on hogchokers from the Hudson River estuary, where the first of bimodal peaks in a frequency distribution of hogchoker lengths corresponded to age-1 fish, whereas the second peak represented combinations of length distributions for fishes age 2–6 yr. Chauvet's (1972) data for *C. canariensis* off West Africa also show a similar pattern of overlapping sizes among fishes of different ages.

Symphurus plagiusa is a good candidate for an age and growth study. It is unique among the Cynoglossidae in that it is the only species of this family that inhabits estuarine environments in the seasonally dynamic region of north temperate latitudes. Most other cynoglossid species occur in the tropics and are difficult to age from hard parts because environmental constancy precludes the formation of interpretable annular growth marks on these structures (Qasim, 1973). Other species of symphurine tonguefishes that occur in temperate waters generally are small-size, deep-water forms that are difficult to catch in abundance (Munroe, 1998).

This study was undertaken to determine age structure, growth rate, longevity, and mortality for a population of *S. plagiusa* residing in Chesapeake Bay, Virginia. Knowledge about life history parameters for this species provides a window of understanding into the biology of the Cynoglossidae, as well as insights into age, growth, and longevity of other small-size, estuarine-dependent flatfishes.

Materials and methods

Blackcheek tonguefishes were collected by 9.14-m semiballoon otter trawl with a 38.10-mm stretch mesh body, 6.35-mm mesh codend liner, and attached tickler chain (Bonzek et al., 1993). Fish were collected from April 1994 through August 1995 during the Virginia Institute of Marine Science (VIMS) Juvenile Finfish and Blue Crab Stock Assessment Program's trawl survey. The survey employs a monthly, random-stratified design of the lower Chesapeake Bay and fixed-station mid-channel transects in each of three major Virginia tributaries: the York, James, and Rappahannock rivers (Fig. 1). Details of sampling design were provided in Geer et al. (1993).

Samples of blackcheek tonguefishes selected from trawl catches were brought to the laboratory, measured for total length (TL) to the nearest millimeter and for total weight (TW) taken to the nearest hundredth of a gram. When samples were small, all fish were used in age analyses; however, fish were randomly selected for age analyses from relatively large samples. Regressions were fitted to the length–weight data, and regressions on log-transformed data for male and female blackcheek tonguefish were compared by using analysis of covariance (ANCOVA). The formula to convert SL to TL for blackcheek tonguefish provided by Jorgenson and Miller (1968:11) was used when comparing length data (reported as SL) from other studies.

All fish were sexed macroscopically, and then gonads were removed and preserved for later histological analysis to determine maturity stages (Terwilliger, 1996). Males were classified as either immature or mature according to the absence or presence of spermatozoa in the testes; females were considered mature if they showed any evidence of developing oocytes or previous spawning, e.g. thickening of the ovarian membrane.

Both sagittal otoliths were removed, cleaned, and stored dry for later processing. Otolith maximum

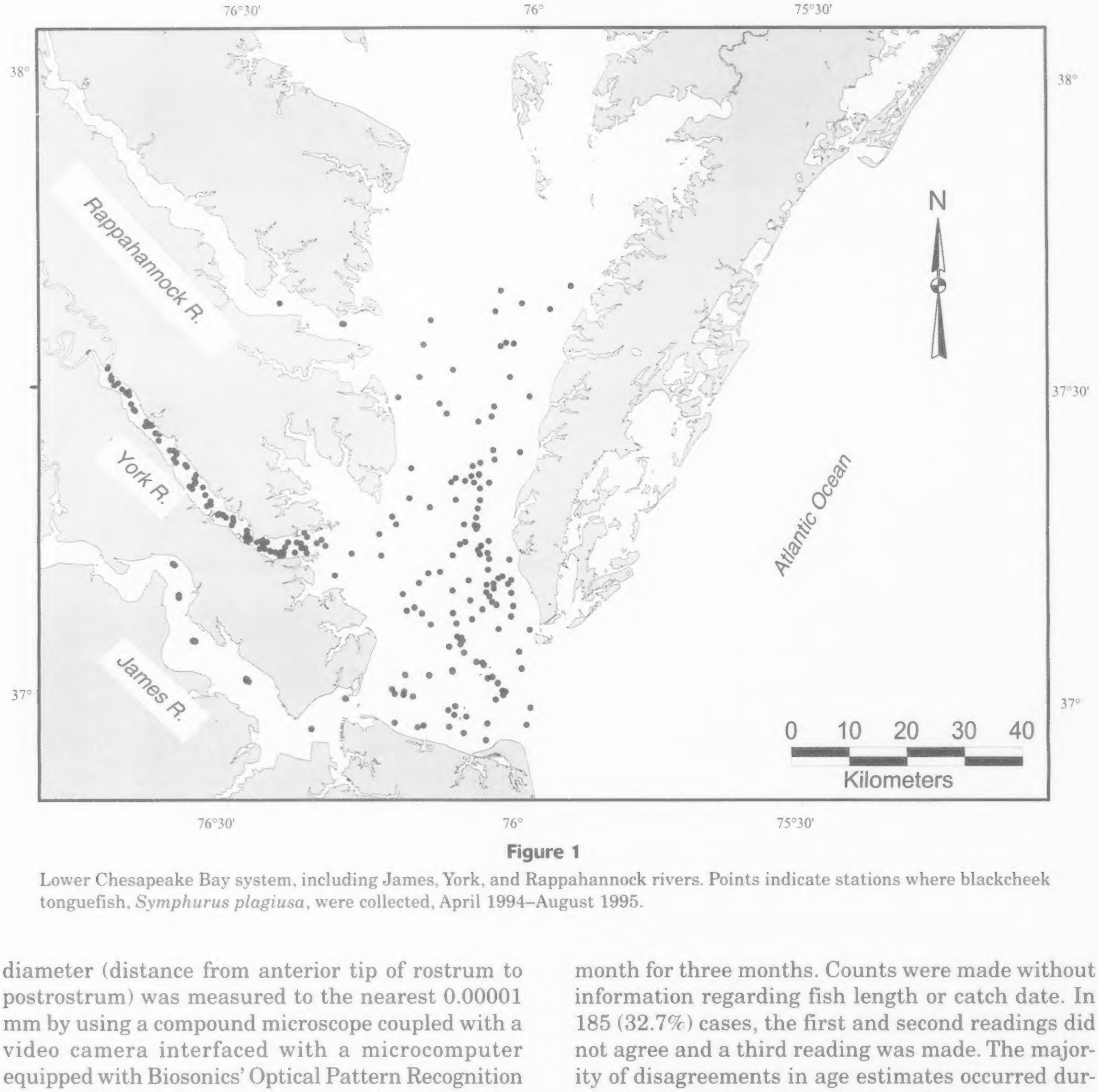

Figure 1

Lower Chesapeake Bay system, including James, York, and Rappahannock rivers. Points indicate stations where blackcheek tonguefish, *Symphurus plagiusa*, were collected, April 1994–August 1995.

diameter (distance from anterior tip of rostrum to postrostrum) was measured to the nearest 0.00001 mm by using a compound microscope coupled with a video camera interfaced with a microcomputer equipped with Biosonics' Optical Pattern Recognition System (OPRS) software (Biosonics, Inc., 1987). Because no asymmetry in otolith shape was apparent, sagittal otoliths (left or right) were arbitrarily selected from each fish for age analysis, embedded in epoxy resin (Spurr, 1969), and sectioned transversely (1 mm thick) through the core with a Buehler Isomet low-speed saw with duel diamond blades. Sections were mounted on glass slides with Crystal Bond adhesive, sanded with 1000-grit sandpaper to remove saw marks and to gain proximity to the core, polished with alumina powder, and examined with a binocular dissecting microscope (30×) with transmitted light and bright field. Annuli on otoliths from all 566 blackcheek tonguefish were counted once a month for three months. Counts were made without information regarding fish length or catch date. In 185 (32.7%) cases, the first and second readings did not agree and a third reading was made. The majority of disagreements in age estimates occurred during the beginning of the study; subsequent re-ageing resolved most discrepancies in age estimates. In most cases, the second reading of an otolith section differed from the first reading by only one year. If a third reading agreed with either of the first two, then that age was assigned to the otolith. In 28 (5%) cases, the third reading was different than the first and second readings. These 28 otoliths were considered unreadable and excluded from further analysis.

Otolith annuli were validated by the marginal increment method (Bagenal and Tesch, 1978; Jearld, 1983). Distances from the core to each annulus and the proximal edge were computed by drawing a vertical line from the core to the proximal edge of the otolith with the OPRS. The average margin width, i.e. the translucent region between the last annulus and the proximal edge of the otolith, was plotted by month.

Regression analyses of otolith maximum diameter on total length and of weight on total length were calculated by the method of least squares. Back-calculated lengths-at-age were computed by using the Lee method (Lagler, 1956). To evaluate growth, back-calculated lengths-at-ages were fitted to the von Bertalanffy model (Ricker, 1975) by using nonlinear regression (Marquardt method) calculated with Fishparm computer software (Saila et al., 1988). Likelihood-ratio tests were used to compare parameter estimates of the von Bertalanffy equation for males and females (Kimura, 1980; Cerrato, 1990).

A scale sample from a region in the posterior third of the body, dorsal to the midline, was taken from all fish. Six scales from each fish were cleaned with hydrogen peroxide and mounted on plastic strips by using a Carver hydraulic laboratory press. A random sample of scale strips from 50 fish were then viewed with a microfiche reader in order to discern annuli for comparison with otolith sections. In contrast to otoliths, scales proved to be unreliable for ageing this species. Annuli were poorly defined and difficult to distinguish, and in many cases, the scales were unreadable. Fish ages obtained from scales agreed with ages obtained from otoliths in only 12% of the cases. This is not surprising, because scale annuli from other fish species with known ages have been shown to be inconsistent indicators of age, even in relatively young fish (Prather, 1967; Heidinger and Clodfelter, 1987).

Instantaneous total annual mortality rates, Z, were estimated from maximum age estimates with a pooled regression equation as suggested by Hoenig (1983) and by calculating a theoretical total mortality for the entire lifespan following the reasoning of Royce (1972) as described in Chittenden and McEachran (1976). Values of Z were converted to total annual mortality rates, A, using the relationship $A = 1 - e^{-Z}$ (Ricker, 1975).

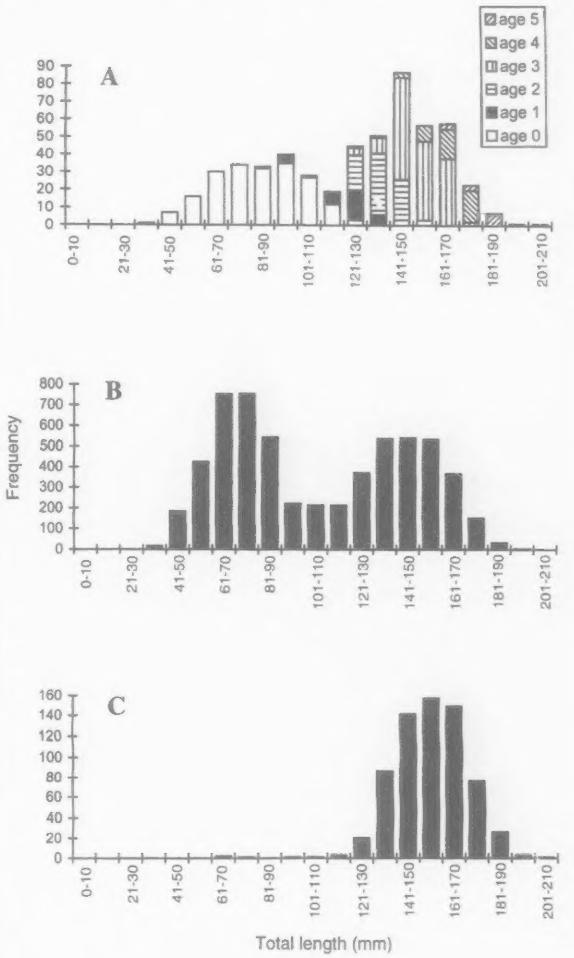

Figure 2

Length-frequency distribution for blackcheek tonguefish, *Symphurus plagiusa*: (**A**) length frequency for blackcheek tonguefish from lower Chesapeake Bay and major lower tributaries for fishes aged in this study; (**B**) length frequency for blackcheek tonguefish caught by Virginia Institute of Marine Science's juvenile fish recruitment trawl survey in lower Chesapeake Bay and major lower tributaries, 1993–1996; (**C**) length frequency for blackcheek tonguefish caught at the mouth of Chesapeake Bay and inner shelf off Virginia and North Carolina, 1987–89.

Results

A total of 566 fish, encompassing a size range from 36 to 202 mm TL (Fig. 2A), were used in this ageing study. This size range included individuals from all life history stages from postsettling juveniles to mature adults. The sex ratio for blackcheek tonguefish collected in this study was 223 males:343 females, or 1:1.54. A G-test of the sex ratio for 566 blackcheek tonguefish indicated statistically significant deviations (G=25.64; df=1; P<0.001) from a 1:1 sex ratio (Table 1). A G-test of sex ratios for blackcheek

Table 1

G-test of sex ratio for blackcheek tonguefish, *Symphurus plagiusa*, caught in lower Chesapeake Bay and three Virginia tributaries, April 1994–August 1995 (**A**) total catch; (**B**) by 25 mm size increment. Yates' correction for continuity implemented in (**B**) due to small sample sizes. *n* = number of fish; df = degrees of freedom; ns = nonsignificant.

A

	Males	Females	*n*	df	*G*	*P*
Frequency	223	343	566	1	25.64	10.83*
Expected	283	283				

* *P*<0.001.

B

Length	Males	Females	*n*	df	*G*	*P*
26–50	7.5	4.5	12	1	0.7580146	ns
Expected	6.0	6.0				
51–75	18.5	36.5	55	1	6.0008514	5.024**
Expected	27.5	27.5				
76–100	46.5	53.5	100	1	0.4904009	ns
Expected	50.0	50.0				
101–125	26.5	44.5	71	1	4.6135656	3.841*
Expected	35.5	35.5				
126–150	68.5	106.5	175	1	8.3175269	7.879***
Expected	87.5	87.5				
151–175	51.5	91.5	143	1	11.339487	10.828****
Expected	71.5	71.5				
176–200	7.5	8.5	16	1	0.0625408	ns
Expected	8.0	8.0				
201–225	0.5	1.5	2	1	0.5232481	ns
Expected	1.0	1.0				

* *P*<0.05; ***P*<0.025; ****P*<0.005; *****P*<0.001.

tonguefish broken down into 25-mm length increments showed that females dominated many intermediate size classes (Table 1).

The length–weight relationships for 200 males (48–190 mm TL) and 310 females (46–202 mm TL) (Fig. 3) were

$$\text{Males: } W = 10^{-5.30}\,(TL^{3.126});$$
$$\text{Females: } W = 10^{-5.37}\,(TL^{3.163}).$$

No statistically significant differences were found between sexes in the total length-total weight relationships (ANCOVA; F=3.86; df=506; P>0.25). The length-weight relationship for sexes combined was

$$W = 10^{-5.34}\,(TL^{3.148}).$$

Size at sexual maturity observed in female and male blackcheek tonguefish ranged between 80–130 mm TL and 70–110 mm TL, respectively. Length at which 50% of the population reached maturity was 101 mm TL for females and 91 mm TL for males (Fig. 4).

Sagittal otoliths of blackcheek tonguefish are small, round, dense structures that cannot be read whole. Transverse sections of otoliths (Fig. 5), however, revealed fairly distinct opaque bands that could be counted. Transverse sections through otoliths indicated that otolith structure consists of an opaque core usually surrounded by a wide opaque area whose outer edge demarcates the first annulus. Size and appearance of this first annulus vary among fish, ranging from a broad band continuous with the core to a narrow opaque band not continuous with the core. Subsequent annuli are represented by thin opaque bands encircling the core and by broader translucent zones found between annuli. At the margin of the otolith, an annulus was difficult to observe. However, when sufficient spring and early summer growth had occurred and contributed translucent material to the margin of the otolith after annulus

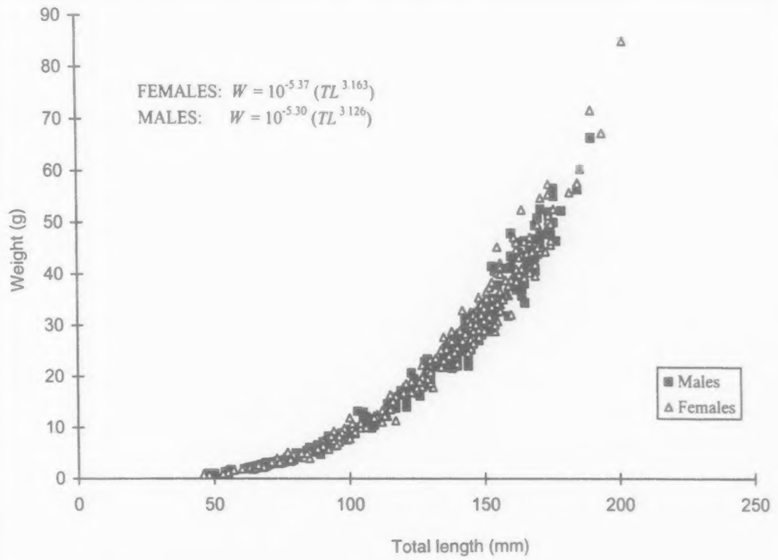

Figure 3

Total length–weight relationship for both sexes of blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries.

formation, the densely compacted opaque zone delimiting the annulus was easily identifiable. The combination of one broad translucent zone and one narrow opaque zone (Fig. 5) represents one year's growth.

Otolith maximum diameter (OMD) was linearly related to total length (Fig. 6) and described by the following relationship:

$$TL = 64.59(OMD) - 17.02. \qquad [r^2=0.93]$$

This linear relationship indicated that otolith growth was proportional to fish growth.

Size at first annulus formation for blackcheek tonguefish ranged from 88 to 138 mm TL (mean length ca. 118 mm TL). Seasonal progression of modal length frequencies (Fig. 7) for young-of-the-year fish (YOY) corroborated first-year growth-rate estimates determined from annular marks on the otoliths. Pooled data for 1993–96 from VIMS[1] trawl survey reports indicated that YOY blackcheek tonguefish recruited to the gear during September, usually at sizes of ca. 35–45 mm TL. By the following June, these fish had reached sizes ranging from ca. 53 to 138 mm TL. Thus, empirical data from length frequencies agreed fairly well with first-year growth estimates derived from interpretation of annulus formation on the otoliths.

Monthly mean marginal increments on the otoliths were plotted for fish from all age groups (Fig. 8). The seasonal progression of marginal increments was similar on otoliths from all age groups; therefore, data were pooled to demonstrate general trends in annual growth. Marginal increments were smallest during June of both 1994 and 1995. Monthly mean marginal increments showed only one trough during a year, indicating that a single annulus is formed yearly in June. In 1994, margin width on the otoliths increased rapidly during July and August, reflecting an active period of growth. After August 1994, margin width leveled off and remained fairly constant from September 1994 through May 1995. Large variation (indicated by high standard error) for samples taken during May of both 1994 and 1995 may indicate that the season of annulus formation may be somewhat more protracted (May–June) and perhaps dependent upon environmental factors. Alternatively, it may simply reflect an artifact of the small sample sizes examined from this period.

Mean lengths at age were backcalculated for 92 males and 145 females (Table 2). Remaining fish were young-of-the-year and therefore were excluded from this analysis. Observed (empirical) lengths were consistently higher than the back-calculated lengths-at-age for individual age groups, which indicated that seasonal growth had occurred since formation of a new annulus. Differences between back-calculated lengths-at-age and observed lengths are in the range of observed seasonal growth. Males and females have similar lengths-at-age until age 4 (Table 2). Beyond age 4, mean lengths for females were slightly greater than those for males. The largest male collected in this study was 190 mm (age 5+); the largest female collected was 202 mm (age 5+).

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[1] VIMS (Virginia Institute of Marine Science), Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

Greatest incremental growth in TL for both sexes occurred during the first year and then declined rapidly thereafter (Table 2). Mean back-calculated lengths for females and males at the end of their first year were 78.84 mm and 75.68 mm, respectively. Growth for both sexes in the second year was only 39–41% of that recorded for the first year. Growth increments continued to decrease every year thereafter for both sexes until age 5, when the estimated growth increment increased slightly for both sexes. This increase at age 5 may be an artifact due to the relatively small number of samples for both sexes in this age group.

Length frequency for blackcheek tonguefish caught by VIMS[2] trawl survey (1993–96) shows a bimodal distribution (Fig. 2B), but this distribution does not adequately reflect age composition of the individuals, especially for fishes larger than 110 mm TL. Despite the bimodal distribution in length frequencies, six age groups are represented in this distribution, and much overlap in total length exists between age groups, especially those consisting of medium- and large-size fish. These data indicate that length frequency analyses are unreliable age estimators for older individuals of this species.

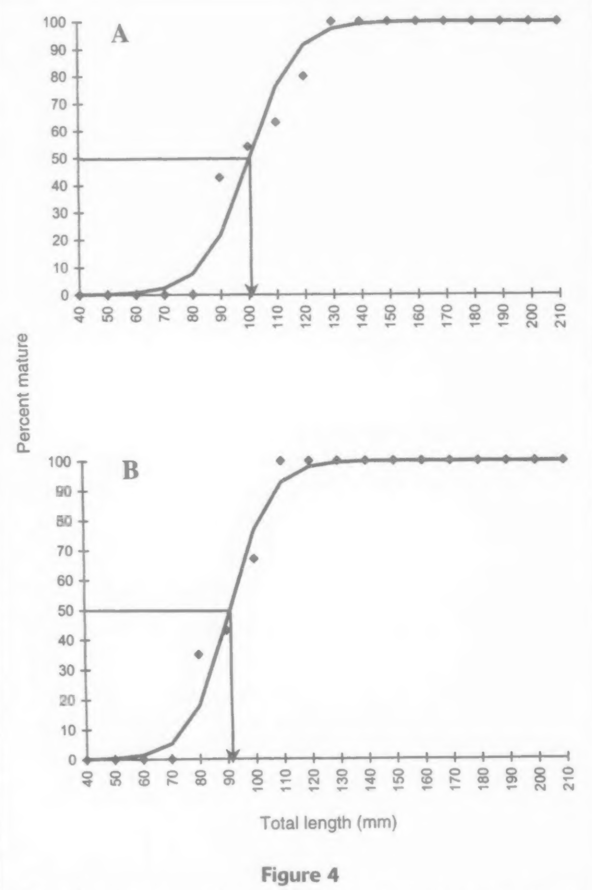

Figure 4

Length at maturity for blackcheek tonguefish, *Symphurus plagiusa*, in lower Chesapeake Bay and major lower tributaries: (**A**) females; (**B**) males. Arrow represents length at 50% maturity.

Von Bertalanffy parameters were computed (Table 3) by using lengths backcalculated to the most recent annuli to reduce bias in asymptotic length and growth coefficient *K* due to the presence of Lee's phenomenon in the back-calculated lengths-at-age (Vaughan and Burton, 1994). The growth coefficient *K* for female blackcheek tonguefishes (0.320) was greater than that (0.285) calculated for males. Males and females achieved 50% of L_∞ by the end of their first year and 75% between ages 2 and 3 (Fig. 9). Results of likelihood-ratio tests (Table 4) showed no significant differences in the overall von Bertalanffy growth models for males and females (χ^2=6.56, df=3, *P*=0.09). Estimates of L_∞ (χ^2=0.10, df=1, *P*=0.75), *K* (χ^2=0.03, df=1, *P*=0.87), and t_0 (χ^2=0.19, df=1, *P*=0.67) were not significantly different between sexes.

Values for asymptotic lengths for both sexes agreed well with observed lengths. The largest male collected in this study was 190 mm and the calculated L_∞ for males was 196.5 mm. The largest female collected in this study was 202 mm and the calculated asymptotic length for females was 190.6 mm. These results are acceptable because asymptotic length is a regression estimate, and thus an average that represents an average maximum length if fish live and grow according to the von Bertalanffy equation. Nevertheless, the overall estimated asymptotic length value (192.4) represents a reasonable approximation of the average maximum length estimate for the species.

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[2] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

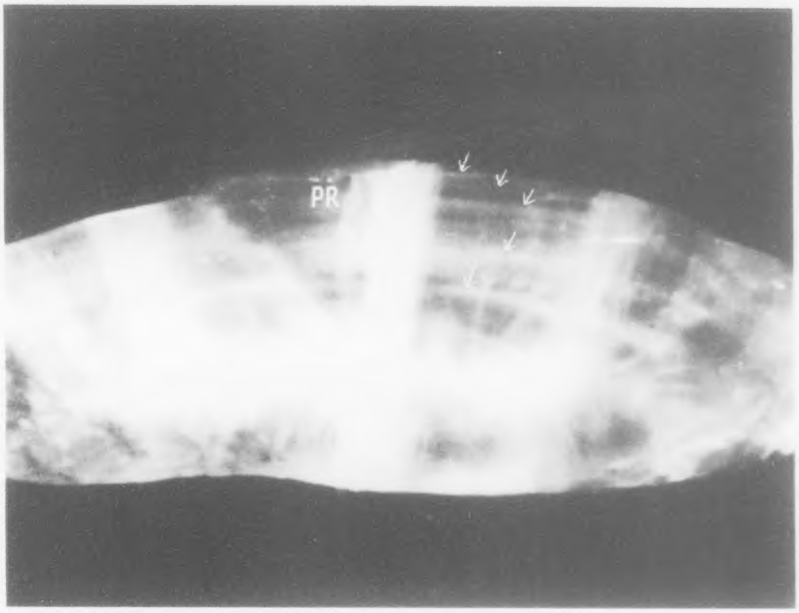

Figure 5

Transverse section from a sagittal otolith of a blackcheek tonguefish, *Symphurus plagiusa*, collected in lower Chesapeake Bay and major lower tributaries. Age 5+. Arrows indicate annuli. Pr = proximal; Ro = rostral.

Table 2

Mean observed and back-calculated lengths for female and male blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay: ages 1–5.

				Mean back-calculated lengths at successive annuli (mm)				
Age	Sample size	Size range (mm)	Mean observed length (mm)	I	II	III	IV	V
Females								
1	15	93–138	121.07	83.943				
2	31	127–155	136.81	81.156	115.272			
3	64	126–170	153.33	76.038	113.238	135.832		
4	25	135–175	161.62	70.073	101.826	126.549	145.385	
5	10	162–202	181.20	82.966	108.644	129.812	150.714	167.936
Mean length				78.835	109.745	130.731	148.049	167.936
Growth increment				78.835	30.910	20.986	17.318	19.887
Males								
1	12	88–125	115.83	81.778				
2	22	103–146	136.59	82.844	113.864			
3	31	130–171	154.19	76.573	110.408	133.553		
4	23	146–179	166.52	73.339	107.662	129.228	148.911	
5	4	162–190	177.75	63.838	95.125	118.058	141.277	163.721
Mean length				75.675	106.765	126.946	145.094	163.721
Growth increment				75.675	31.090	20.182	18.147	18.628

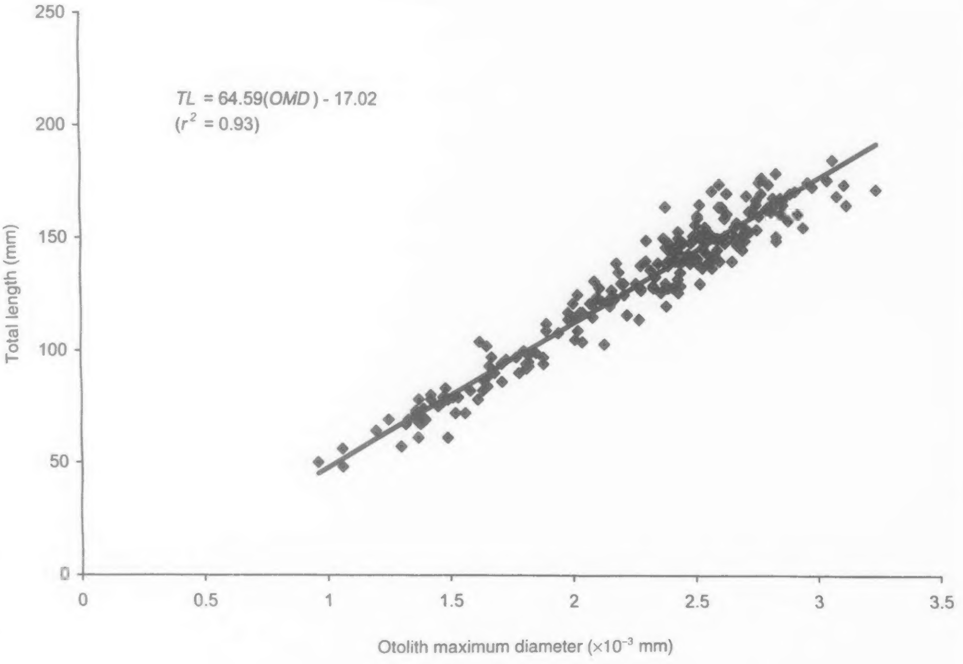

Figure 6

Linear regression of total length (mm) on otolith maximum diameter (mm) for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries.

Instantaneous total mortality (Z) estimates obtained for a maximum age of 5 years were 0.87 (A=58%) with Hoenig's (1983) method, and 0.92 (A=60%) with Royce's (1972) method. A plot of age composition of the catch (Fig. 10) indicates rapidly declining numbers of fishes aged 4 and 5.

Discussion

Most of what we know regarding growth in cynoglossid flatfishes stems from information gathered from studies conducted on species of *Cynoglossus*. These are tonguefishes usually much larger in size than species of *Symphurus* (Menon, 1977), and species which also occur predominantly in the shallow tropical seas of the Indo-West Pacific. Therefore, the present study detailing information on age, growth, and longevity for blackcheek tonguefish is significant in being the first of its kind reporting such life history parameters for a member of *Symphurus*. Furthermore, of the approximately 150 species of Cynoglossidae, *S. plagiusa* is unique in that it is the only member of the family inhabiting temperate estuarine environments in the seasonally dynamic Chesapeake Bay region of the western North Atlantic. In fact, the tonguefishes inhabiting Chesapeake Bay are the northernmost major population of this species (Munroe, 1998). Here, the species has ranked as high as sixth in overall abundance, and in some years is the second most abundant pleuronectiform among fishes taken during trawling in lower Chesapeake Bay and its tributaries (Geer et al., 1993). North of the Chesapeake Bay region, adult blackcheek tonguefish are relatively rare (Munroe, 1998), even in such proximate estuaries as Delaware Bay. Just how long the Chesapeake Bay has supported a significant population of this species is unknown because earlier compilations on fishes of the region (Hildebrand and Schroeder, 1928) regarded this species as occurring only rarely within the Bay. It is conceivable that because of its relatively small size and benthic habits, the abundance of this species may have been grossly underestimated during previous fish surveys conducted in this region. However, given the general rarity of this species in areas immediately to the north, and the observed incidences of winter mortalities within Chesapeake Bay (see be-

Table 3

Von Bertalanffy parameters and equations calculated for male and female blackcheek tonguefish, *Symphurus plagiusa*, collected in Chesapeake Bay, Virginia. Values in parentheses are standard errors.

Parameter	Males	Females	Combined
K	0.285	0.320	0.308
	(0.075)	(0.061)	(0.047)
L_∞	196.5	190.6	192.4
	(20.04)	(13.03)	(10.88)
t_0	−0.920	−0.784	−0.832
	(0.289)	(0.216)	(0.172)
Equation	$L_t = 196.5\,(1 - e^{-0.285(t + 0.920)})$	$L_t = 190.6\,(1 - e^{-0.320(t + 0.784)})$	$L_t = 192.4\,(1 - e^{-0.308\,(t + 0.832)})$

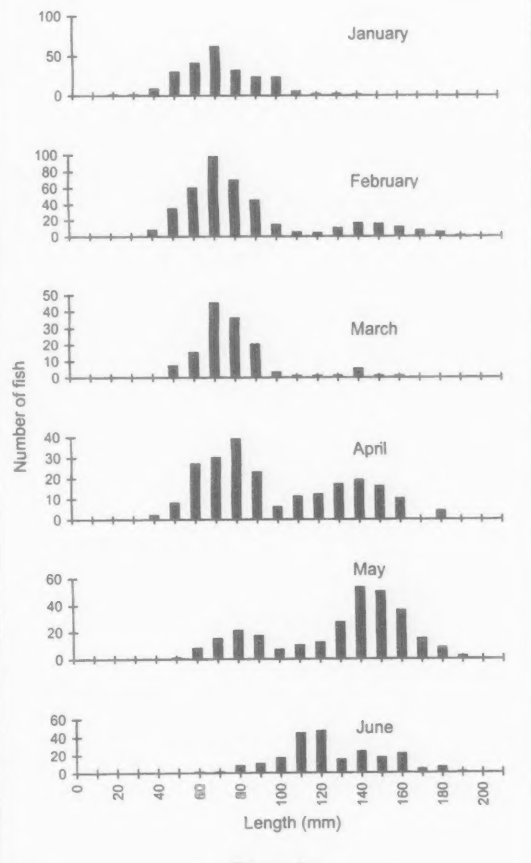

Figure 7

Seasonal progression of modal length frequencies for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries, 1993–96.

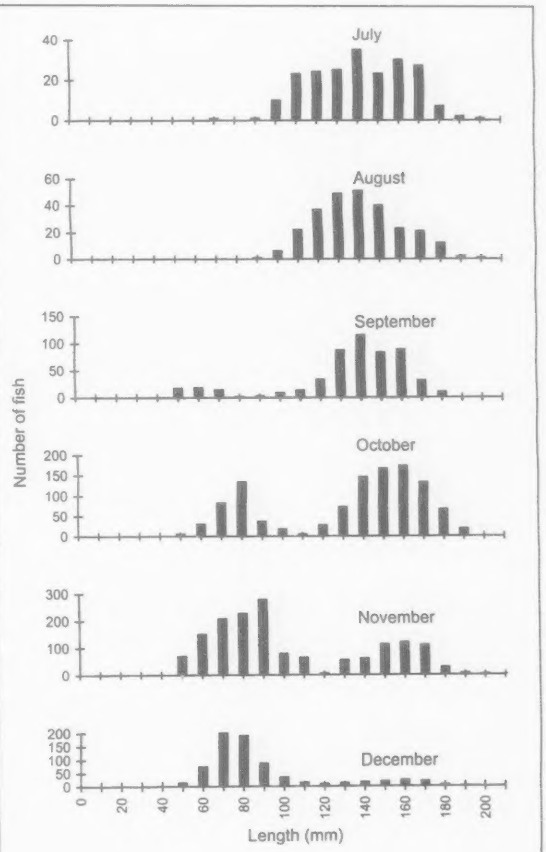

Figure 7 (continued)

low), it also seems equally possible that the population of blackcheek tonguefishes residing in Chesapeake Bay could be of more recent origin because all other major populations for this species are known to occur only in areas further to the south. If indeed this is the case, then life history parameters estimated for blackcheek tonguefishes from Chesapeake Bay are those characterizing a peripheral population of the species. Comparisons of these estimates of life history parameters, then, with values derived from other, more centrally located, populations of this species, as well as with those from populations inhabiting subtropical environments in northern Mexico and Cuba (Munroe, 1998), would prove interesting from the perspective of discovering the range of variability in life history features that has evolved within this species of flatfish.

Sizes of blackcheek tonguefishes collected within Chesapeake Bay during the present study represent almost the complete size range known for the species (Munroe, 1998). The largest female (202 mm TL) and largest male (190 mm TL) taken within the Bay approach the largest sizes known for this species (ca. 210 mm TL; Wenner and Sedberry, 1989). However, most blackcheek tonguefishes occurring within this system were smaller, with total lengths usually ranging between 35 and 150 mm. The size range for blackcheek tonguefishes occurring in Chesapeake Bay is not unlike those reported for other estuarine populations located throughout the species' range. For example, Shealy et al. (1974) reported that, during a year-long survey of fish assemblages in South Carolina estuaries, blackcheek tonguefishes ranged in size from 53 to 156 mm TL. However, modal lengths for this species were never greater than 140 mm TL, and fish were usually much smaller (monthly mean size 97–124 mm TL). In fact, of the blackcheek tonguefishes taken during that study, only 8 of 362 (2.2%) were 150 mm TL or larger.

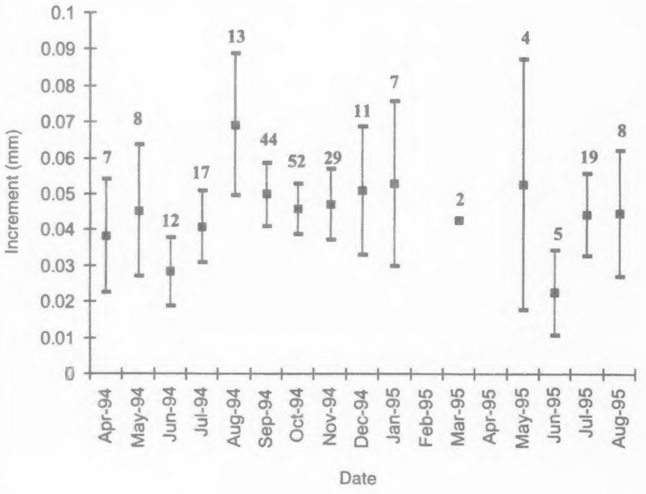

Figure 8

Plot of monthly mean marginal increments for blackcheek tonguefish, *Symphurus plagiusa*, ages 1–5, collected in lower Chesapeake Bay and major lower tributaries. Vertical bars represent ±1 standard error. Numbers above bars represent monthly sample sizes.

Although many studies (summarized in Munroe, 1998) have reported catching large blackcheek tonguefish from neritic habitats on the inner continental shelf throughout the species' range, size ranges for these fishes were not unlike those observed for blackcheek tonguefishes collected within Chesapeake Bay. For example, blackcheek tonguefishes (n=439) collected at the mouth of Chesapeake Bay and on the inner continental shelf off southern Virginia and northern North Carolina (VIMS[3]) during a series of cruises conducted during 1987–89 ranged from 68 to 203 mm TL (mean size= 154.5 mm TL; Fig. 2C); and most fishes

Table 4

Likelihood ratio tests comparing von Bertalanffy parameter estimates for male (1) and female (2) blackcheek tonguefish, *Symphurus plagiusa*, from Chesapeake Bay, Virginia. df = degrees of freedom.

Hypothesis	Linear constraints	Residual SS	χ^2_r	df	P
HΩ	none	99,760.5			
Hω1	$L_{\infty 1} = L_{\infty 2}$	99,780.9	0.1043	1	0.7467
Hω2	$K_1 = K_2$	99,765.8	0.0271	1	0.8692
Hω3	$t_{01} = t_{02}$	99,796.9	0.1861	1	0.6661
Hω4	$L_{\infty 1} = L_{\infty 2}$ $K_1 = K_2$ $t_{01} = t_{02}$	10,051.6	6.558	3	0.0874

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[3] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

measured 140–180 mm TL. Lengths of fishes collected within the Bay system completely overlap those taken from the nearby shelf. Munroe (1998) noted that most blackcheek tonguefishes in collections from throughout the species' geographic range were usually much smaller than the largest sizes known for the species because only 4% of 568 fish he examined exceeded 164 mm TL. Wenner and Sedberry (1989) sampled 8780 blackcheek tonguefishes from coastal habitats (<10 m depth) between Cape Fear, North Carolina, and the St. Johns River, Florida, and reported that length composition of trawl-caught *S. plagiusa* was consistent from season to season, with mean sizes ranging between 140–150 mm TL. The largest specimens taken during that study were 210 mm TL, and few fish <100 mm TL were caught, possibly because fish smaller than this inhabited a different habitat as juveniles or because they did not recruit to the fishing gear until 100 mm TL. On the continental shelf off Tampa Bay, Florida, lengths (124–174 mm TL) for blackcheek tonguefishes were also similar to those reported for fish from Chesapeake Bay (Moe and Martin, 1965).

Although age estimates are not available for other populations of blackcheek tonguefish, a general comparison of growth between blackcheek tonguefishes occurring in Chesapeake Bay with those from other areas is provided by examination of length–weight parameters derived for different populations. Dawson (1965) generated a length-weight relationship for 3504 blackcheek tonguefish (43–148 mm TL) occurring in Gulf of Mexico waters. With this relationship, weights were generated from 510 randomly selected lengths between 43 and 148 mm TL and these were then compared with a similar number of weights generated for fishes of the same size range by using the length-weight relationship derived for blackcheek tonguefishes from Chesapeake Bay. No significant differences ($t=0.53$; df=1010; $P=0.60$) were evident in this comparison between weights of fishes of these two regions, indicating that growth in weight, at least, is similar for fishes of this size range occurring in these widely separated areas within the species' range.

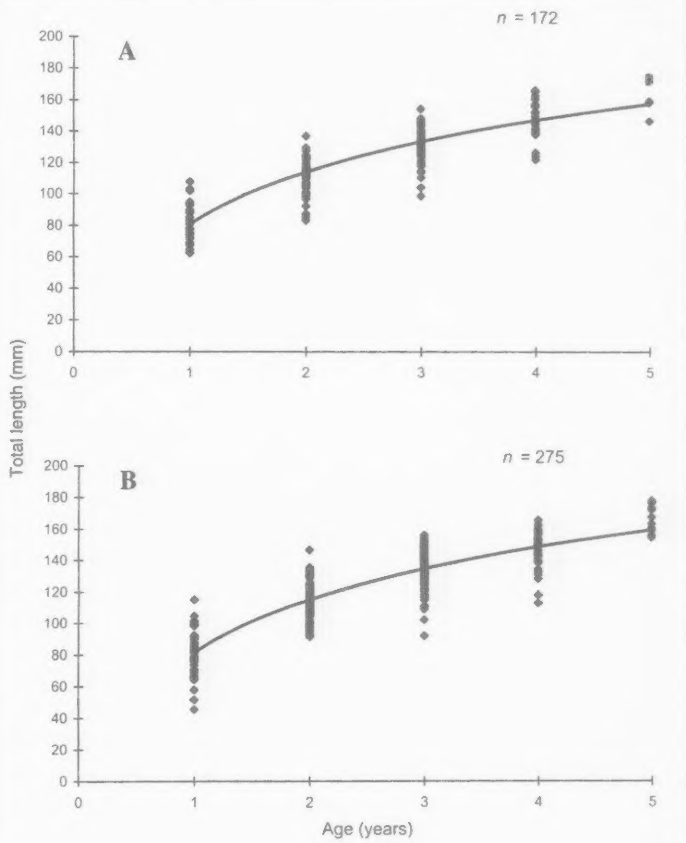

Figure 9

Plot of back-calculated and predicted lengths from the von Bertalanffy growth model for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries: (**A**) males; (**B**) females.

Annuli form on the otoliths of blackcheek tonguefishes from late spring through early summer (mostly June), coincident with the summer warming period and also at the initiation of the spawning season (Terwilliger, 1996). For *C. abbreviatus,* a tonguefish occurring in temperate seas off eastern China (Zhu and Ma, 1992), annuli form on otoliths during March–May, a period also corresponding to seasonal timing of gonad maturation and warming of water temperatures. Koski (1978) reported that annuli form on scales of hogchokers in the Hudson River from April to mid-June, which is a period of increasing water temperature, and for mature fish this also corresponds to the time just prior to and overlapping the early spawning season.

Flatfishes typically exhibit sexual dimorphism in size at age (Roff, 1982; and others, see below)—

females usually growing larger than males. In the Chesapeake Bay population, male and female blackcheek tonguefishes attain similar maximum sizes (mean value for oldest females=181.2 mm TL; mean value for oldest males=177.8 mm TL). In summarizing size information for blackcheek tonguefishes collected throughout the geographic range of the species, Munroe (1998) also reported no significant size differences between males (to 174 mm TL) and females (to 172 mm TL). For 23 other species of western Atlantic tonguefishes, females reached larger sizes than males in 11 of these species, in six others a larger size was reported for males, whereas in seven other species similar maximum sizes were attained by both sexes (Munroe, 1998). However, since no age estimates have been made for these other species of *Symphurus,* comparative data on dimorphism in lengths at age for these symphurine tonguefishes are unavailable. For other cynoglossids with accompanying age data, considerable variation exists in the degree of sexual dimorphism evident in sizes attained by the sexes. In the Malabar sole (*Cynoglossus semifasciatus*) off India, females grow larger than males, although reported differences in maximum sizes between sexes were relatively small (Seshappa and Bhimacher, 1954). Similarly, although female *C. abbreviatus* (to 348 mm TL) from Jiaozhua Bay, China, were larger than males (to 321 mm TL), average total lengths at age between the sexes were not significantly different (Zhu and Ma, 1992). Females of *C. bilineatus* and *C. arel* were also reported to be larger than males sampled from the same populations (Hoda and Khalil, 1995), whereas sizes for adult female (83–173 mm TL) and male (84–168 mm TL) *C. macrostomus* were found to be similar (Victor, 1981). Female *C. canariensis* also grow larger than males (Chauvet, 1972). For *C. semilaevis* inhabiting the Bohai Sea, China (Meng and Ren, 1988), quite a different situation exists. In this species, females attain lengths (to 638 mm TL) slightly more than twice those reached by males (to 312 mm TL). In other estuarine flatfish, such as the hogchoker, which occurs throughout much of the geographic range of the blackcheek tonguefish, females grow to larger sizes than do males from the same population (Koski, 1978). For most species of the Pleuronectidae, females also typically grow larger and have both a later age and larger size at maturity than do males (Cooper[4]).

Back-calculated lengths-at-age for blackcheek tonguefishes were consistently less than observed lengths-at-age for all age groups combined, which may be attributed to Lee's phenomenon. The principal cause of Lee's phenomenon in unexploited fish populations, such as that of blackcheek tonguefish inhabiting Chesapeake Bay, is that faster growing fish tend to mature and die earlier than do smaller members of the same year class (Gerking, 1957; Ricker, 1975). When a larger proportion of older fish die, the result is a smaller estimated size for fish at younger ages than the true average size at the age in question. Since blackcheek tonguefishes are not harvested commercially or recreationally within the Bay, the presence of Lee's phenomenon in the back-calculation estimates may be due to higher mortality of larger individuals within an age class, or possibly this finding may reflect the fact that larger fish move out of the Bay system and onto the nearby shelf region. The ages of blackcheek tonguefishes occurring on the continental shelf throughout the species' range are unknown. No offshore samples of blackcheek tonguefishes were collected during this study, and it is unknown if any of these fish are older than those occurring in Chesapeake Bay.

Although female blackcheek tonguefishes captured in Chesapeake Bay grew at a slightly faster rate than did males, observed differences in back-calculated lengths between male and female blackcheek tonguefishes beyond age 4 were not statistically significantly different. However, our sample sizes for older fish were small and interpretation of data for this oldest age class is limited. In other cynoglossids, such as Malabar sole, faster growth has also been observed in females compared with that for males (Seshappa and Bhimachar, 1954). Rajaguru (1992) found that female *C. arel* grew faster than males, but no significant differences in growth patterns were found between female and male *C. lida*. After their first year, female hogchokers in the Hudson River also grew faster than males (Koski, 1978). In some species of the Soleidae, such as the Agulhas sole (*Austroglossus pectoralis*) occurring off South Africa (Zoutendyk, 1974) and *Solea solea* in Spanish waters (Ramos, 1982), females also have a faster growth rate than do males within the same populations. A faster growth rate for females compared with that of males has also been reported in a variety of other flatfish species (Chen et al., 1992; Santos, 1994).

Estimates of the growth parameter *K* (Table 5) for blackcheek tonguefish are relatively high, indicating that these fish reach their asymptotic length relatively rapidly (Francis, 1996). Few estimates of *K*-values are available for other tonguefishes, but for those species studied, growth rates are relatively high. Where data are available, all, except two species, have higher growth coefficients reported for females. In *C. arel*, *K*-values were 0.315 for females and 0.238 for males, and in *C. lida* *K*-values of 0.233

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[4] Cooper, J. A. 1998. National Marine Fisheries Service, National Systematics Laboratory, Washington, DC 20560. Personal commun.

for females and 0.223 for males were reported (Rajaguru, 1992). For *C. abbreviatus* (Zhu and Ma, 1992), *K*-values were 0.395 for females and 0.344 for males. In two of the largest species in the family, *C. semilaevis* and *C. canariensis*, the estimated *K*-values were higher for males compared with those for females. In *C. semilaevis*, *K*-value for females was 0.264, and that of males was 0.352 (Meng and Ren, 1988). For female *C. senegalensis* the *K*-value was 0.32 compared with 0.36 for males (Chauvet, 1972).

Table 5

Comparision of von Bertalanffy parameters of selected Pleuronectiformes occuring in temperate estuaries of the western North Atlantic.

Species	Parameters	Source
Paralichthys dentatus (♀♂)	K: 0.215 L_∞: 859 mm t_0: –0.690	Desfosse, 1995
Paralichthys lethostigma (♀)	K: 0.235 L_∞: 760 mm t_0: 0.570	Miller et al., 1991
Scophthalmus aquosus (♀)	K: 0.272 L_∞: 383 mm t_0: 0.418	Miller et al., 1991
Pseudopleuronectes americanus (♀)	K: 0.217 L_∞: 375.8 mm t_0: 0.730	Miller et al., 1991
Symphurus plagiusa (♀♂)	K: 0.308 L_∞: 192.4 mm t_0: –0.832	Terwilliger, 1996
Trinectes maculatus (♀)	K: 0.195 L_∞: 209.5 mm t_0: –0.353	Miller et al., 1991

In Chesapeake Bay, blackcheek tonguefishes achieve most of their growth in length during their first year. Males and females attained up to 50% of their total growth in length by the end of their first year, and up to 72% of their total growth by the end of their second year. Such rapid first-year growth does not appear to be unusual among members of the Cynoglossidae. For example, male *C. arel* grew between 180–194 mm TL, and females from 201–210 mm TL, during their first year (Rajaguru, 1992), which represented up to 58% and 51% of their total growth in length (333 and 393 mm, respectively). Similar to the pattern observed in blackcheek tonguefish, second-year growth in this species was estimated to be only 18% and 21% of the total growth, respectively, for males and females. In *C. lida*, males (151–154 mm TL) and females (153–156 mm TL) also reached fairly large sizes during their first year of life, with first-year growth for males and females ranging between 69 and 71% of the total growth in length (216 and 218 mm, respectively), compared with second-year growth values of only 13–14% of the total length (Rajaguru, 1992). *Cynoglossus macrolepidotus* also has a high growth rate during its first year, reaching a length of about 160 mm TL, and like the preceding species, during the second and subsequent years there occurs a marked reduction (only 10–30 mm increase/yr) in growth rate (Kutty, 1967). Likewise, in *C. abbreviatus* (Zhu and Ma, 1992), first-year growth is maximal for both sexes (males to 162 mm TL, females to 178 mm TL; representing 50% and 51% of total growth, respectively), whereas second-year growth in this species averages only about 16% or less of the total growth. This growth pattern was also apparent for *C. canariensis* where male and female fish, respectively, achieved 50% and 55% of their total growth in length during the first year, compared with second-year growth equalling only 14–15% of the total growth in length (Chauvet, 1972). In another large-size species, *C. semilaevis*, first-year growth is also rapid, with males reaching 141 mm TL at end of year one and females growing to 194 mm TL, values that represent 45% and 30% of the total growth in length achieved by this species (Meng and Ren, 1988). However, in contrast to other cynoglossid species examined thus far, growth in this species during the second year differs markedly between the sexes. For females, the average growth increment during the second year was greater than that of the first year (to 307 mm TL, 36% of total growth in length), whereas during this same time interval males averaged only about one-half of the growth increment attained during year one (to 204 mm TL, representing 20% of total growth). In the hogchoker, growth in length is also rapid; males and females achieve 56% and 44% of their total growth in length during the first year (Koski, 1978). By the end of their second year, hogchokers have reached on average 74% (males) and 63% (females) of their total growth in length.

The substantial reduction in growth rate beyond age 1 noted for blackcheek tonguefishes occurs at a time coincident with maturation (Terwilliger, 1996). Roff (1982) noted that, for fish in general, it is frequently observed that rate of growth decreases with the onset of maturity. This slowing in somatic growth may reflect an allocation of energy to gonadal development, or may be a response to other physiological processes associated with maturation. Other cynoglossid species that have been aged also mature sexually at a relatively early age even in some of the larger-size species. Seshappa and Bhimachar (1954) reported that young Malabar soles (*C. semifasciatus*) grew to adult size within a year or less and that after maturation, growth slowed distinctly. After an initially high growth rate during their first year, there also occurred a marked reduction in the growth rate of *C. macrolepidotus* during their second year, at a time coincident with initiation of the spawning season (Kutty, 1967). Likewise, in other cynoglossids (*C. arel* and *C. lida*) occurring off India, growth during the first year is also rapid and this fast growth period is then followed by a considerable reduction in the growth rate during the next year when the fishes matured sexually (Rajaguru, 1992). In *C. arel*, for example, which reaches total lengths to 333 mm SL, males and females mature at sizes of about 217 mm TL and 225 mm TL, respectively, sizes reached by this species at the beginning of their second year of life. In *C. lida*, size at 50% maturity is 167 mm TL for males, and 179 mm TL for females. These represent sizes that are reached by the fish during the beginning of their second year of life. For *C. dubius* (Seshappa, 1976) minimum size at maturity was reported to be about 287 mm TL for females, a size that corresponded to fish approximately 2–3 years old. In *C. canariensis*, a species reaching total lengths of 486 mm (males) and 519 mm (females), maturity occurs at about 1.5 years when fish are about 300 mm TL (Chauvet, 1972).

Hoenig's and Royce's mortality estimates, based on the maximum known age of a species, indicate a relatively high instantaneous total mortality in the blackcheek tonguefish population inhabiting Chesapeake Bay (Table 6). Relatively few of the blackcheek tonguefishes within Chesapeake Bay are older than three years. The age structure observed in this population may, however, reflect the relatively short life span of this species (5+ years), or it could also reflect high mortality levels experienced by blackcheek tonguefishes in the Bay environment; undoubtedly it would also be influenced by the emigration of larger individuals from the Bay system.

Relatively short life spans may be typical of species of *Symphurus* and of the Cynoglossidae, in general. In fact, some dwarf species of tropical *Symphurus* reach maximum sizes of only 35–45 mm SL (Munroe, 1990, 1998) and probably live no more than a year. Age estimates based on growth marks interpreted from scales of tonguefishes occurring in coastal waters off India indicate that Malabar sole reach an age of only about 2+ years (Seshappa and Bhimachar, 1954). Based on studies of tonguefishes from the west coast of India, a life span of 3–4 years was reported by Seshappa (1978, 1981) for *C. lida* (size to 220 mm TL; most 140–189 mm TL) and *C. puncticeps* (to 209 mm TL; most 90–179 mm TL), whereas a life span of 6+ years (to 339 mm TL; most 160–299 mm TL) was reported for *C. bilineatus* from the same region. More recently, Rajaguru (1992) reported that *C. arel* and *C. lida* along the southeast coast of India have life spans just over 3 years. For *C. dubius* off India (to 414 mm TL), age estimates were 6+ years for most individuals, although some individuals reached 10 years (Seshappa, 1976). *Cynoglossus arel* off Taiwan (Lin, 1982) live to be at least 4 years. Kutty (1967) reported a maximum age of 6–7 years for *C. macrolepidotus* (to 330 mm TL). For *C. canariensis* (to 519 mm TL) off tropical West Africa, both sexes live to at least 8 years (Chauvet, 1972). For the temperate species, *C. abbreviatus*, from Jiaozhua Bay, China (Zhu and Ma, 1992), which is commercially exploited, females reach 8 years and males live to 7 years, and total mortality for this population was estimated to be very high (0.607). For

Table 6

Mortality estimates (*Z*) for various northwestern Atlantic Pleuronectiformes based on Hoenig's and Royce's equations. Values in parentheses reflect extrapolated mortality rates for a possible seventh age class of blackcheek tonguefish, *Symphurus plagiusa*, found in lower Chesapeake Bay and the inner continental shelf.

Species	Maximum age	Hoenig's equation	Royce's equation	Data source
Winter flounder (*P. americanus*)	14 years	0.32	0.33	Lux, 1973
Summer flounder (*P. dentatus*)	9 years	0.49	0.51	Desfosse, 1995
Windowpane (*S. aquosus*)	7 years	0.62	0.66	Moore, 1947
Southern flounder (*P. lethostigma*)	6 years	0.73	0.77	Music and Pafford, 1984
Hogchoker (*T. maculatus*)	6 years	0.73	0.77	Mansuetti and Pauly, 1956
Blackcheek tonguefish (*S. plagiusa*)	5 years (6 years)	0.87 (0.73)	0.92 (0.77)	Terwilliger, 1996

C. semilaevis from Chinese waters, a strong sexual dichotomy in longevity was apparent in the population studied; females reached 14 years (most 2–8 years), whereas males in this population attained a maximum age of only 5 years (Meng and Ren, 1988). By comparison, longevity estimates for a variety of other flatfishes occurring in temperate latitudes and from families other than the Cynoglossidae range from 6 to 30 years (Devold, 1942; Arora, 1951; Pitt, 1967; Lux and Nichy, 1969; Lux, 1970, 1973; Koski, 1978; Wada, 1970; Zoutendyk, 1974; Smith and Daiber, 1977).

As stated earlier, the population of *S. plagiusa* in Chesapeake Bay represents the northernmost location of a major population of this species (Munroe, 1998). In the western North Atlantic, variability in abiotic conditions increases from southern to northern latitudes (Parr, 1933; Miller et al., 1991). Abiotic variability also increases in environments located closer to the shoreline (Russell-Hunter, 1970; Miller et al., 1991). Fluctuations in abiotic factors, especially seasonal extremes of temperature during winter, may contribute to the high level of total instantaneous mortality measured for blackcheek tonguefishes within Chesapeake Bay. Bottom trawls conducted in this system during late winter and early spring of some years (1996, for example) catch numerous dead and moribund tonguefishes (Geer[5]), apparently due to stresses associated with extremely cold water temperatures (ca. 2°C. in 1996). More extreme winter temperatures and longer duration of cold temperatures may be a factor limiting the establishment of populations of blackcheek tonguefishes in more northern estuaries, where this species is known only by the occurrence of newly settled juveniles. In coastal estuaries throughout its U.S. geographic range, blackcheek tonguefishes appear to be sensitive to extreme winter temperatures, because winter mortalities have also been reported for this species in estuaries even as far south as those in Texas (McEachron et al., 1994). In addition to causing death outright, stresses associated with extreme winter temperatures may also render weakened tonguefishes easier prey to predators and thus further contribute to winter mortalities.

Mortality estimates for the population of blackcheek tonguefishes residing in Chesapeake Bay may also be inflated due to emigration of larger individuals out of the Bay and onto the nearby continental shelf. Hildebrand and Cable (1930) earlier had suggested that adult blackcheek tonguefishes in North Carolina estuaries undergo a seaward migration during May–August. An autumn emigration of blackcheek tonguefishes from Chesapeake Bay to the nearby shelf region just outside of the Bay may be reflected in the significantly larger catches (mean no./tow) of blackcheek tonguefishes reported (VIMS[6]) in this region during fall sampling (1987, 75.4/tow; 1988, 25.7/tow) compared with springtime catches (1987, 11.0/tow; 1988, 4.37/tow; 1989, 2.2/tow). Data supplied in Wenner and Sedberry (1989) also support the hypothesis that there is a seasonal migration of larger tonguefishes out of estuaries and onto the coastal shelf off South Carolina. They reported that this species was widespread throughout the survey area but noted that significant seasonal differences were apparent in the frequency of occurrence and abundance of *S. plagiusa* in coastal habitats. This species occurred less frequently during winter (48% of all tows; 566 individuals) than in spring (85% of tows; 1,460 individuals), summer (76% of tows; 798 individuals), or fall (94% of tows; 5962 individuals). Catches (mean no./tow) of this species were lowest in summer (8/tow) and winter (9/tow), higher in spring (21/tow), and highest during the fall (62/tow), when the largest fish (up to 210 mm TL) were taken. Although Wenner and Sedberry (and other studies) have reported that it is usually only larger-size blackcheek tonguefishes that are captured on the inner shelf region, no studies have verified any seasonal or spawning movements of blackcheek tonguefishes out of the estuaries, or the amount of exchange of individuals within populations between estuarine embayments and adjacent neritic habitats on the inner shelf. It is also unknown whether all larger individuals undergo an ontogenetic migration out of estuaries onto the nearby shelf; what portion of a population residing in estuaries moves out onto the shelf at any given age; what the estuarine residency time is for larger tonguefishes, especially in such larger and deeper estuaries as the Chesapeake Bay which may be utilized by larger tonguefishes for longer periods of time; or even if further exchange of individuals between these two environments occurs once an individual has emigrated beyond the estuarine boundary. Analysis of catch curve data (Fig. 10) may also lend insight on inflated mortality estimates. Although the bimodality of the catch curve data infers possible variability in year-class strength that invalidates its use for mortality estimations (Robson and Chapman, 1961; Everhart and Youngs, 1981), the data suggest that a seventh year class may exist, possibly on the nearby shelf region. If so, mortality estimates based on a maximum age of 5+ years would be inflated compared with those calculated for an older year class.

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[5] Geer, P. J. 1996. VIMS, Department of Fisheries, Gloucester Point, VA 23062. Personal commun.

[6] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

Sex ratio of tonguefishes sampled during this study deviated from 1:1 mostly due to large single-sex catches of females during the summer months in the lower Bay. In lower Chesapeake Bay, apparently some spatial separation of the sexes occurs (Terwilliger, 1996). Here, dense concentrations of female blackcheek tonguefishes were commonly found in the deeper areas, and fewer males were taken in the same trawls. Among sympatric species of pleuronectiforms, the hogchoker also reportedly displays bathymetric separation of the sexes in tributaries of Chesapeake Bay during the summer months prior to spawning (Mansuetti and Pauly, 1956), when females occupy grass beds and shoal regions, while males are surmised to occupy deeper areas within the estuary. This pattern of habitat segregation by adult hogchokers, however, was not evident in the study conducted by Koski (1978) in the Hudson River, although he noted that although the overall sex ratio for fishes examined did not differ from 1:1, some individual trawl catches were dominated by or consisted entirely of one sex. Significant differences in the sex ratios of catches of other tonguefishes have also been reported. Seshappa and Bhimachar (1955) noted that sex ratios of catches of Malabar sole during the spawning period were markedly different than those made during other times of the year and attributed these differences to differential behavior of the two sexes during their spawning migrations. Hoda and Khalil (1995) also reported skewed sex ratios (1.0:2.55 males to females) for catches of *Cynoglossus arel*, whereas those (1.16:1) for *C. bilineatus* were not significantly different from 1:1. A skewed ratio (1.56:1) favoring females over males was also found for *C. semilaevis* (Meng and Ren, 1988). Although some studies have inferred spatial differences in movements of the different sexes of cynoglossid tonguefishes based on fisheries catch data, it is difficult to draw any general conclusions from these data. Just as we lack reliable documentation concerning spatial movements for the two sexes of blackcheek tonguefish, directed studies providing the detailed information necessary for interpreting adult movements of any of these other cynoglossid species have yet to be performed.

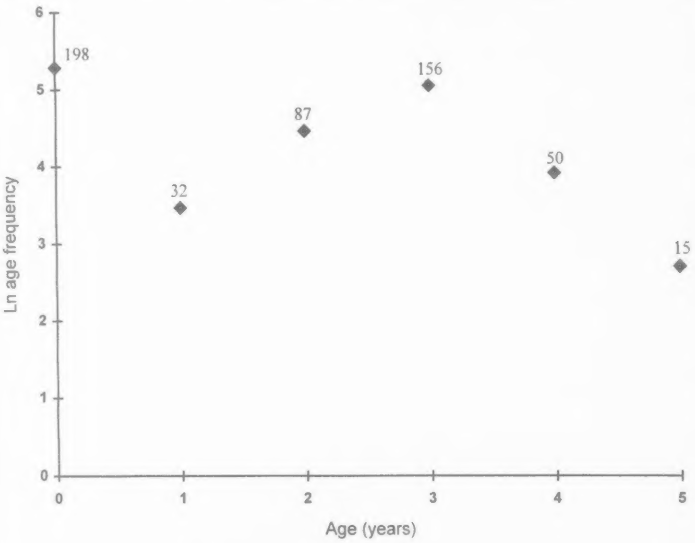

Figure 10

Catch curve for blackcheek tonguefish, *Symphurus plagiusa*, collected by otter trawl in lower Chesapeake Bay and major lower tributaries, 1993–95. Numbers above plot represent numbers at each age.

North temperate estuaries, such as Chesapeake Bay, are rigorous physical systems well known for environmental extremes in temperature, salinity, and dissolved oxygen, and for strong seasonal cycles of primary and secondary production. However, the extensive distribution within the Bay and its tributaries of shallow, soft bottom sediments presents considerable amounts of suitable habitat for flatfishes. Twelve species of flatfishes have been recorded from the Bay (Murdy et al., 1997). The unique geographical location of Chesapeake Bay at the northern end of a warm temperate and southern end of a cold temperate region (Briggs, 1974) may account for the occurrence within the Bay of diverse faunal components, which have either warm or cold water affinities. Among pleuronectiforms inhabiting Chesapeake Bay, for example, are six species representing five different families (Cynoglossidae, Achiridae, Paralichthyidae, Scophthalmidae, and Pleuronectidae). This assemblage includes representatives of families whose species occur primarily in cold temperate or boreal areas (Scophthalmidae, Pleuronectidae) or in warm temperate and tropical regions (Cynoglossidae, Achiridae, Paralichthyidae). Of the species occurring within Chesapeake Bay are blackcheek tonguefish, hogchoker, and smallmouth flounder, *Etropus microstomus* (to ca. 159 mm TL), small-size species that are not commercially or recreationally exploited and ones that complete their life cycles within the Bay. Virtually nothing is known concerning age and growth of smallmouth flounder, especially within the Bay system; therefore further comparisons of its life history with those of sympatric flatfishes are limited. The flatfish fauna of the Bay also includes summer flounder (*Paralichthys dentatus*), southern flounder (*Paralichthys lethostigma*), windowpane (*Scophthalmus aquosus*), and winter flounder (*Pseudopleuronectes americanus*), species that do not necessarily complete their life cycles entirely within Chesapeake Bay and ones that are heavily exploited both commercially and recreationally. The remaining species of flatfishes recorded from the Bay are transient species that occur only irregularly within the Bay and will not be discussed further. The diversity in size and growth parameters represented among those flatfishes occurring in Chesapeake Bay which have been studied provides an interesting opportunity for investigating comparative life histories of sympatric members of an estuarine benthic fish assemblage with somewhat similar lifestyles (Table 5).

Few published age-growth studies exist for noncommercially exploited flatfishes, especially for those species occurring in temperate estuaries of the western North Atlantic. Von Bertalanffy growth parameters for species other than blackcheek tonguefish were taken from data found in the literature (Miller et al., 1991; Desfosse, 1995). These data reveal that among this assemblage, blackcheek tonguefish have the highest value for growth parameter K (Table 5), and therefore reach asymptotic length faster than sympatric counterparts (Francis, 1996). Of sympatric flatfishes occurring in Chesapeake Bay, only hogchokers display growth parameters and maturation schedules (some males mature at end of first year, most of both sexes mature by age 2; Koski, 1978) similar to those observed for blackcheek tonguefish. In contrast, summer and southern flounders mature at ages 2–3, windowpane flounders mature at ages 3 or 4, and winter flounders mature at ages 2–5. Later age at maturation in these species reflects a different life history pattern, and one that allows for energy allocation favoring increased somatic growth during several years prior to the onset of maturation. Because these other species mature at later ages than do blackcheek tonguefish and hogchoker, growth in length for these fishes would be relatively rapid over the course of several years during the early part of their lives (Fig. 11).

Estimates of asymptotic length, reflecting average maximum length attained by a species, also varies considerably among members of this assemblage. Asymptotic lengths for summer flounder (859 mm TL) and southern flounder (to 760 mm) greatly exceed those for blackcheek tonguefish and hogchoker (192 and 210 mm, respectively). In fact, these fishes grow more during their first year than do blackcheek tonguefish and hogchokers in a lifetime. Windowpane and winter flounder (383 and 376 mm, respectively) attain asymptotic lengths intermediate to these other two groups of sympatrically occurring estuarine flatfishes.

Estimates of instantaneous total mortality based on blackcheek tonguefishes caught within Chesapeake Bay during this study are also relatively higher when compared with those for most other estuarine dependent species of northwestern Atlantic Pleuronectiformes (Table 6). In this comparison, blackcheek tonguefish are among the shortest-lived species and therefore have one of the higher rates of instantaneous total mortality. Relatively few individuals within Chesapeake Bay are older than three years. Extrapolating mortality rates for a possible seventh year class (age 6+), which may be found on the inner shelf region, provides an instantaneous total mortality estimate comparable to those for hogchokers and southern flounder caught in Chesapeake Bay.

Blackcheek tonguefish exhibit the youngest age at first maturity, the highest growth coefficient, the youngest known maximum age, and the smallest asymptotic length when compared with sympatric pleuronectiforms from Chesapeake Bay. Blackcheek tonguefish exhibit rapid growth until maturity, after which growth rate declines markedly. Munroe (1990, 1998) indicated that eight dwarf species of *Symphurus* reach sexual maturity between 28 and 45 mm SL. Small size and presumably early age at maturation may be characteristic of species in this genus (Munroe, 1988); even *S. jenynsi*, the largest species in the genus (reaching ca. 350 mm TL), matures at a relatively small size (about 132 mm TL). More ageing studies on fishes of this genus are required to test this hypothesis. Other cynoglossid flatfishes, although they attain a relatively large size before reaching sexual maturity, are only 1 or 2 yr old when first maturing. According to available data, it is quite possible then that tonguefishes in general have an age dependent maturity schedule. Roff (1982) indicated that age, and not size, would appear to be most important in fish species that mature early. Data for tonguefishes support that finding.

When compared with estimates for sympatric flatfishes, blackcheek tonguefish caught during this study exhibit the highest rates of instantaneous total mortality. Other species inhabiting the Bay system also mature at larger sizes, have larger asymptotic lengths, and slower growth rates. Interesting

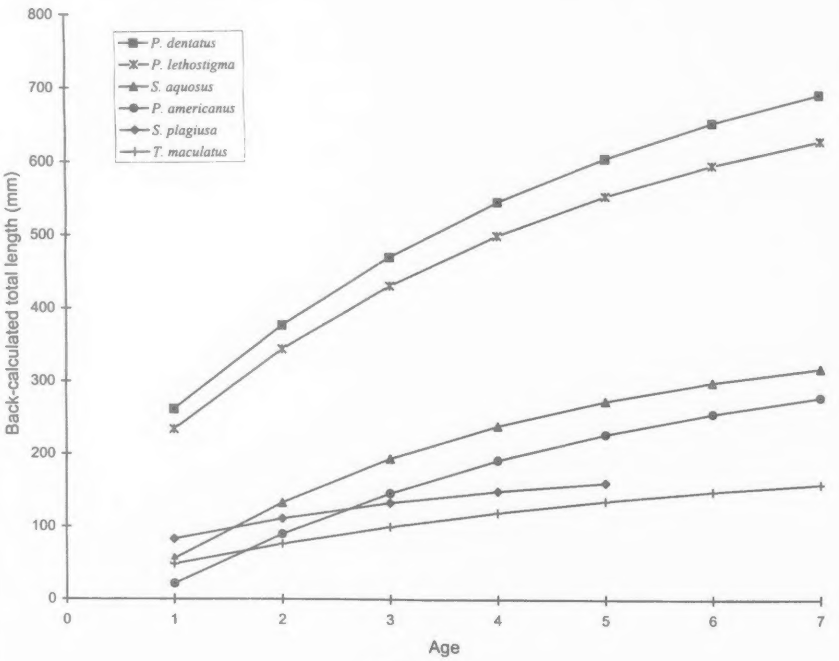

Figure 11

Von Bertalanffy growth curves for selected Pleuronectiformes occurring in western North Atlantic temperate estuaries. Values for species other than *Symphurus plagiusa* were derived from the literature.

to note, it is only the smallest-size and shortest-lived flatfishes (*S. plagiusa*, *T. maculatus*, and probably *E. microstomus*) that complete their life cycles within Chesapeake Bay. Under an environmental regime with a large component of unpredictable, nonselective mortality, an organism is hypothesized to allocate a larger portion of its resources to reproductive activities (Adams, 1980). Life history parameters, such as rapid growth, small body size, early age at maturity and relatively short life span, characteristics featured in these small-size flatfishes completing their life cycles within Chesapeake Bay, are consistent with those observed for other fish species that survive in and successfully exploit seasonally dynamic and highly unpredictable environments.

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Age distribution and growth of greater amberjack, *Seriola dumerili*, from the north-central Gulf of Mexico*

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Abstract.–The lack of age and growth estimates and population parameters for the amberjack family prompted our study to describe otolith structure and determine size-at-age and growth rates of greater amberjack (*Seriola dumerili*) from the north-central Gulf of Mexico.

Greater amberjack age and growth was described from a combination of external ridges and internal annuli in sectioned sagittal otoliths. A mark-recapture study using tetracycline was consistent with a single annulus being formed each year in two- and three-year-old amberjack. Tag-recapture data from the Gulf of Mexico and South Atlantic Cooperative Gamefish Tagging Program also confirmed that a single annulus increment was formed each year. Ages for 597 specimens ranged from young-of-the-year to 15 years, and all fish over 9 years were female. Sagittal weight provided a reliable estimation of fork length with a relationship of $FL = 151\,(1 - e^{(-0.04(SW+1.6))})$: a negative exponential equation in the form of the von Bertalanffy equation. The fit of the negative exponential in this application provides evidence of the disassociation between otolith growth and fish growth as fish age. The von Bertalanffy growth curve equation, $L_t = 138.9\,(1 - e^{-0.25(t+0.79)})$, compared favorably with previous published values. Monthly changes in size and availability indicate a Gulf-wide migration of this moderately long-lived pelagic predator.

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The greater amberjack, *Seriola dumerili*, is a pelagic reef species ranging along the American coasts from Nova Scotia to Brazil and occurring throughout the Atlantic, Pacific, and Indian oceans, as well as the Mediterranean Sea (Mather, 1958; Burch, 1979; Shipp, 1988). It is the largest member of the family Carangidae (Hoese and Moore, 1977).

Commercial landings of amberjack (all species) have increased markedly over the past twenty years. Landings in the Gulf of Mexico peaked in 1988 reaching 2.7 million pounds, with a dockside value over 1.6 million dollars, but have since declined to less than one million pounds in 1995–96. Recreational catch statistics are incomplete but are suspected to have equalled or surpassed the commercial catch, raising concern over the status of the Atlantic stock in the late 1970s (Berry and Burch, 1979). Despite their popularity as a recreational and commercial quarry, little is known about the life histories of amberjacks (Shipp, 1988).

Of particular concern to stock-assessment scientists is the lack of age and growth estimates and population parameters for the amberjack family (Burch, 1979; Humphreys, 1986). Burch (1979), using scales, aged greater amberjack from the western Atlantic to 10 years for females and to eight years for males. Females were significantly longer than males beyond age four. Humphreys (1986) reported von Bertalanffy growth parameters for Hawaiian greater amberjack but did not elaborate on how the fish were aged or how many fish were contained in the data set.

The purpose of this study was to collect and describe greater amberjack otoliths, assess their utility in age estimation, and determine the size-at-age and growth rates of greater amberjack from the north-central Gulf of Mexico.

Materials and methods

Sampling

Greater amberjack (n=840) were collected off the Louisiana coast from April 1989 to June 1992. Sources of samples included a commercial processor plant (n=18), charterboats (n=352), saltwater fishing tournaments (n=215), spearfishing tournaments (n=159), recreational catches (n=48), and hook-

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and-line catches from an offshore gas production platform (n=48). In general sampling was not systematic; we examined all fish available.

Morphometric measurements and otoliths were collected. Fish were measured by using fork and total lengths (FL and TL) in mm and weighed by using total and gutted weights in g. Both sagittae were removed and stored in 95% ethanol for later examination. Lapilli, asterisci, and dorsal spines were removed from several fish to evaluate their usefulness for age estimation. Otoliths were cleaned of organic tissue by rinsing in a 50% hypochlorite solution (Clorox), air dried, weighed to the nearest 0.1 mg with a Sartorius model 1801 microbalance, and stored dry (Wilson et al.,1991).

Age estimates were made by using techniques similar to those of Wilson et al. (1991) for billfish. Whole otoliths were sputter coated with a mixture of gold and palladium and viewed with reflected light under a dissecting microscope for description of external morphology. These samples were also viewed with a Cambridge Stereoscan 150 scanning electron microscope (SEM) to obtain detailed photographs at magnifications ranging from 20 to 650×.

Sagittae were embedded in epoxy resin (Spurr, Embed 812, or Araldite GY 502) and sectioned with a Buehler Isomet low-speed saw to yield a thin (about 1-mm) transverse section containing the core (Beckman, 1989). Transverse sections were ground with various grades (300–2000 grit) of wet and dry sandpaper until the core was at the surface, then polished with 0.3 µm alumina polish. Thin sections were mounted on glass slides with a clear thermoplastic cement (Crystalbond 509) and viewed under transmitted light with an Olympus BH-2 compound microscope at 50–250× magnification. Age estimates from sectioned sagittae were made by combining counts of translucent and opaque zones and other growth features viewed under transmitted light and counts of associated ridges on the ventral and medioventral portions of the rostrum as determined in billfish species (Wilson and Dean, 1983; Prince et al., 1986; Wilson et al., 1991).

Validation and verification of our age estimation technique were attempted by using several techniques. Validation of annulus formation using marginal increment analysis proved futile owing to our inability to determine the condition of the otolith edge. Therefore we pursued additional techniques that would corroborate our age estimates. A mark-recapture study was carried out from a gas production platform (Mobil USA, West Cameron block 352) located in the Gulf of Mexico 50 miles south of Cameron, Louisiana. Greater amberjack (n=48) were captured by hook and line, measured as described above, tagged at the base of the dorsal fin with a Hallprint dart tag, injected with oxytetracycline hydrochloride (Agrimycin-100) at a rate of 20–40 mg/kg fish weight, and released. Tagged greater amberjack (6) were recaptured with hook and line or by spear fishermen at the release site and sampled as described above. Sectioned sagittae were viewed under ultraviolet light (405–435 nm wavelength) at 50–250× magnification for detection of the tetracycline mark. Attempts made to compare age estimates from sagittal otoliths with dorsal and anal spines and vertebrae were not successful. To determine reproducibility of age estimates, sagittae were aged independently by two readers. Reproducibility of age estimates was compared by using the coefficient of variation (CV) and index of precision (D) (Chang, 1982).

Tag-recapture data for the Gulf of Mexico and South Atlantic (n=711) were obtained from the Cooperative Gamefish Tagging Program (CGTP). Fish that had been at large for at least 365 days after tagging and that showed positive growth were used. Twenty-five specimens met these criteria. Following the method of Labelle et al. (1993), we used the von Bertalanffy growth curve parameters to predict changes in length from the tag recapture data to verify our age estimates. Like Labelle et al. (1993) we employed Fabens' (1965) length increment model to predict length at recapture:

$$lr_i = l_i + (L_\infty - l_i)(1 - e_i^{-k\Delta t}),$$

where l_i = length at release of individual i;
Δt_i = time of liberty of individual i;
lr_i = estimated length-at-recapture of individual i; and
L_∞ and k = von Bertalanffy parameters estimated from otolith ages.

Predicted recapture lengths were then compared with observed recapture lengths. As Labelle et al. (1993) pointed out, this procedure is not statistically rigorous but is useful for comparative purposes.

An analysis of variance (ANOVA) was used to test for sex-related differences in mean fork length, mean gutted weight, mean sagittal weight, and mean age among sources and within age class. Analysis of covariance (ANCOVA) was used to test for differences in the relations (fork length [L] versus total weight [Wt], fork length versus sagittal weight [SW], age versus sagittal weight) between sexes (Cerrato, 1990; Kimura, 1980). Statistical inferences were made with a significance level of α=0.05. The relationship between fork length and otolith weight was modeled with a negative exponential (von Bertalanffy) because it provided the best fit (highest r^2).

The von Bertalanffy model $L_t = L_\infty(1 - e^{-k(t-t_0)})$ was also used to describe the relation between length and age. Relative ages were assigned to fish by using a birth date of 1 April based on trends in gonadosomatic indices and the regression of sagittal weight on month of capture for young-of-the-year fish.[1] Von Bertalanffy growth parameter estimates for males and females were compared by using a likelihood ratio test at $\alpha = 0.05$ (χ^2 statistic) (Cerrato, 1990; Kimura, 1980).

Results

Length and weight

Greater amberjack ranged from 167 to 1441 mm (FL); females ranged from 374 to 1441 mm ($\bar{x}$=879 mm), and males ranged from 387 to 1203 mm ($\bar{x}$=854 mm). Females represented 72% of the fish over 1 m in fork length. There was no significant difference in mean fork length between males and females. Females ranged from 0.82 to 42.5 kg ($\bar{x}$=11.33) and males ranged from 0.85 to 28.8 kg ($\bar{x}$=9.90). Mean gutted weight (GW) of females was significantly greater than that of males (ANOVA $P>F$= 0.03) and females represented 78% of the fish over 20 kg gutted weight. Regressions for TL versus FL and TW versus GW were

$$TL = 1.14\,FL + 13.05 \qquad (r^2=0.99)$$
$$TW = 1.09\,GW + 119.40. \qquad (r^2=0.99)$$

Monthly mean fork length and sex ratio from charterboat catches were compared because this was the only year-round source of greater amberjack (Table 1). Charterboats fishing Gulf of Mexico waters off the Louisiana coast caught larger greater amberjack during the summer months (from May to September) and smaller greater amberjack during winter months (from November to February). Sex ratios ranged from 0.4:1 to 4.5:1 ($\bar{x}$=2.49) (Table 1), and there was a relatively greater abundance of females each month except September.

The relation between fork length (cm) and gutted weight (kg) was best described by a power function. The slopes of the regression lines for males and females were significantly different. The equations explaining these relations were

$$\text{All samples:} \quad W = 4.2 \times 10^{-5}\,L^{2.83} \quad (r^2=0.99,\ n=862)$$
$$\text{Females:} \quad W = 3.25 \times 10^{-5}\,L^{2.87} \quad (r^2=0.98,\ n=324)$$
$$\text{Males:} \quad W = 1.75 \times 10^{-5}\,L^{2.96} \quad (r^2=0.98,\ n=184)$$
$$\text{Sex unknown:} \quad W = 7.62 \times 10^{-5}\,L^{2.87} \quad (r^2=0.98,\ n=354)$$

Table 1

Monthly mean fork length (mm) and sex ratio of charterboat-caught greater amberjack from the northern Gulf of Mexico ranked by decreasing mean fork length.

Month	Mean fork length (mm)	n	Sex ratio female:male
May	771.1	70	2.0
Jul	702.7	11	1.6
Jun	651.0	21	2.7
Sep	613.2	14	0.9
Mar	566.9	75	2.3
Apr	560.4	43	3.5
Nov	482.6	38	2.0
Oct	420.8	59	2.0
Feb	408.4	9	5.0
Dec	383.0	9	0.0
Jan	351.5	2	0.0

Otolith structure

Greater amberjack sagittae are small, thin, fragile, and elongate in the anterior direction and bluntly crenelate at the posterior end. The medial surface is convex and has a deep, prominent sulcus. The anterior portion of the sagitta is curved laterally and the posterior end is relatively flat. The rostrum is longer than the antirostrum, but the difference increases with fish size. Prominent grooves and ridges are present on the lateral side of the sagittae and are nearly absent on the medial side (Fig. 1). The asteriscus and lapillus were much smaller and more fragile than the sagittae and have no annuluslike external or internal growth features. The small size and fragility of these smaller otoliths, as well as the time and care required to remove them, precluded additional sampling.

Greater amberjack sagittae weights ranged from 1.4 to 68.6 mg. The mean weight of male sagittae (23.2 mg) was not significantly different from that of females (25.0 mg). The relationship between FL and sagittal weight (SW) was best described with a negative exponential (following the von Bertalanffy equation). Because there was no difference in this relation between males and females ($P>\chi^2>0.05$) the data were combined to produce the equation (Fig. 2)

$$FL_{\mathrm{SW}} = 151\,(1 - e^{(-0.04(\mathrm{SW}+1.6))}), \qquad (r^2=0.96)$$

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[1] Thompson, B. A., C. A. Wilson, J. H. Render, M. Beasley, and C. Cauthron. 1992. Age, growth, and reproductive biology of greater amberjack and cobia from Louisiana waters. Final report to U.S. Department of Commerce, Marine Fisheries Initiative (MARFIN) Program, NMFS, St. Petersburg, FL, NA90AA-H-MF722, 77 p.

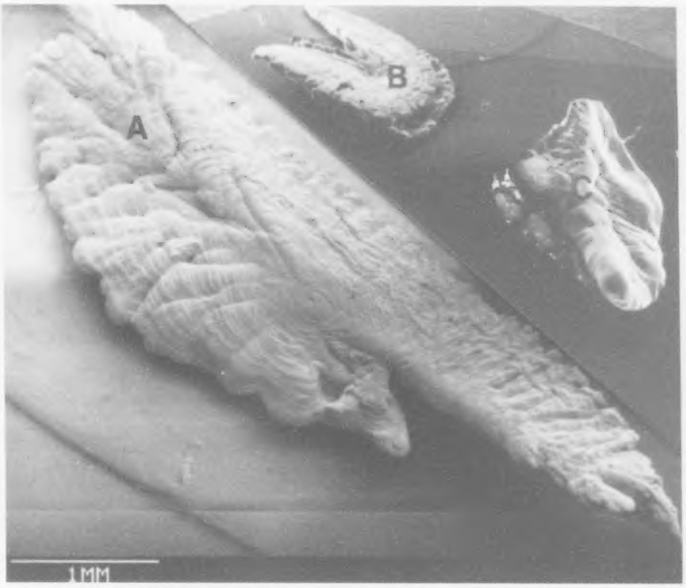

Figure 1

Scanning electron micrograph of a sagitta (lateral view) (**A**), lapillus (**B**), and asteriscus (**C**) from a 42.7-cm greater amberjack from the north-central Gulf of Mexico.

where FL_{SW} = fork length (cm); and
SW = sagittal weight (mg).

Although internal annuluslike features were visible in whole otoliths, they were not sufficiently translucent to permit consistent enumeration. Readability was not improved by immersing sagittae in either glycerin or clove oil for up to one year. Surface grooves and ridges were prominent on the lateral side of sagittae from young fish but became compressed and indistinguishable in older specimens owing to an over-burden of calcium carbonate; a similar observation was reported for marlin (Wilson et al., 1991). External ridges were closely associated with internal microstructure that we interpreted as annuli. Although a first and second annulus was visible in whole sagittae, we concluded that annuli could not be enumerated from whole otoliths for most fish, particularly larger specimens.

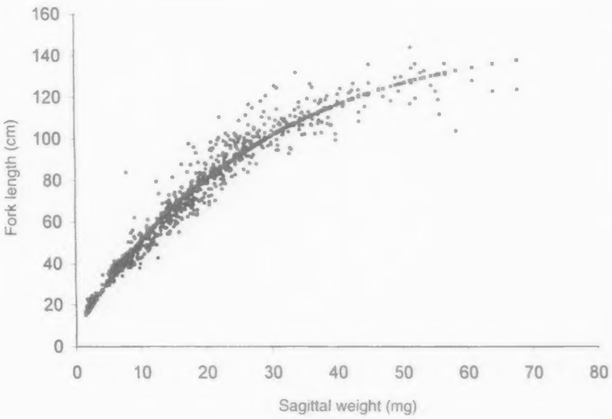

Figure 2

Sagittal weight (mg) versus fork length (cm) for north-central Gulf of Mexico greater amberjack. *x* represents predicted values from given equation.

Microstructural growth features were readily visible in most sectioned sagittae; however, the only consistent annuluslike features were regions where growth bands converged on the lateral side of the otolith section. These "convergence zones" were internal to the lateral surface of the antirostrum, where numerous growth features (increments) converged on a common point (Fig. 3A); these features were usually associated with ridges on the lateral side of the sagitta or associated with alternating opaque and translucent zones, or with both ridges and zones (Fig. 3B). Similar structures were described and used to age istiophorids by Prince et al. (1986) and Wilson et al. (1991).

Six of 48 oxytetracycline-injected fish were recovered from the tag-recapture experiment. Oxytetracycline marks were observed in sectioned sagittae from all six fish (Fig. 4). The location of the oxytetracycline mark in relation to presumed annuli supported the use of the growth features described above.

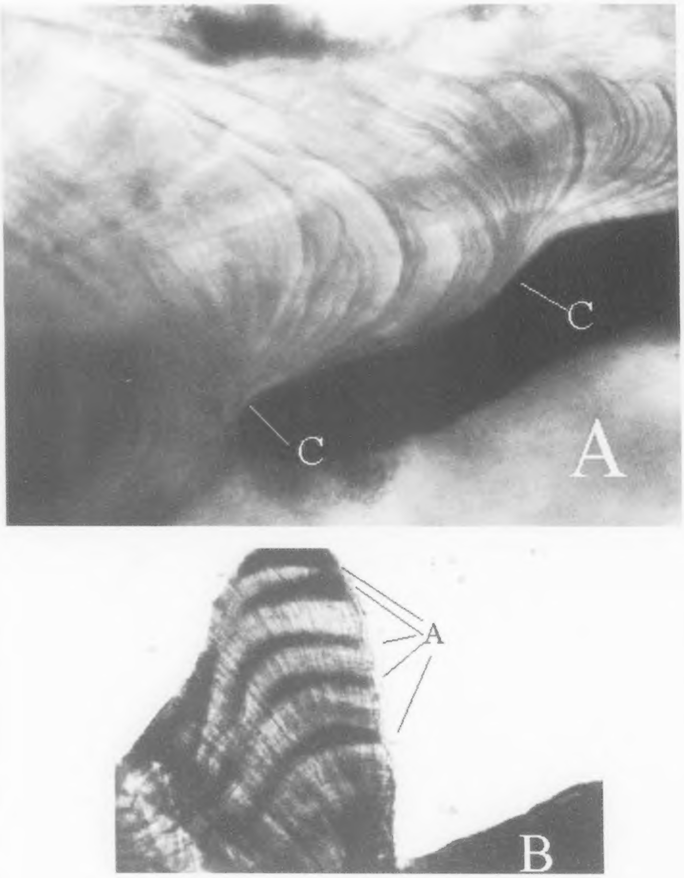

Figure 3

Photomicrographs of sectioned sagittae from a 72-cm-FL (**A**) and 42-cm-FL (**B**) north-central Gulf of Mexico greater amberjack. Photomicrograph A shows the convergence zones (C) along the dorsolateral edge of the rostrum. Photomicrograph B shows the opaque and translucent zones in the rostrum; opaque zones were interpreted as annuli (A).

The specimen in Figure 4 was captured in September and recaptured in March and had an annulus consisting of a ridge and convergence zone between the tetracycline mark and the margin. The combined information obtained from six oxytetracycline-marked otoliths confirmed that one annulus is formed between November and March in the sagittae of two- and three-year-old greater amberjack.

Age structure

Five hundred and ninety seven greater amberjack sagittae were sectioned and aged by two readers. Forty-five specimens were considered unreadable owing to poor sample preparation. Pairwise comparisons between two readers indicated that 9.6% of the counts differed by 1 year, 1.6% differed by 2 years, and 0.4% differed by more than 2 years. Readers combined had a coefficient of variation (CV) of 0.15 and an index of precision (D) of 0.11.

Age estimates of greater amberjack ranged from young-of-the-year to 15 years. Mean age of males (2.9 yr) was not significantly different than that of females (3.2 yr) (ANOVA $P>F=0.064$); however, all fish over 9 years of age were female. Most of the greater amberjack sampled were from one to three years old (Fig. 5).

A linear function best described the relation between estimated age and sagittal weight. The regression parameters were not significantly different (ANCOVA) between males and females; therefore data were pooled and produced the relation

$$Age = 0.15(SW) - 0.44, \quad (r^2=0.75)$$

where SW = sagittal weight (mg); and
Age = amberjack age in years.

Growth was modeled by using the von Bertalanffy growth model (Fig. 6) to facilitate comparisons with other values reported in the literature. Our age data from

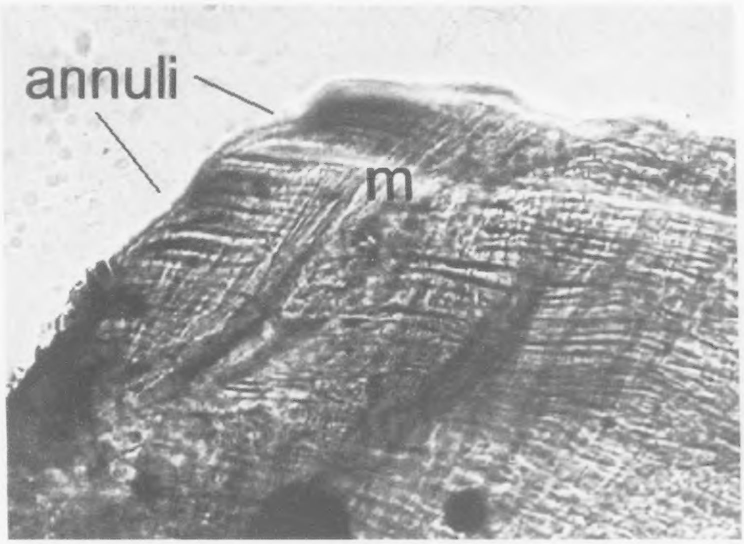

Figure 4

Photomicrograph of a sectioned sagitta from a 53-cm tagged and recaptured north-central Gulf of Mexico greater amberjack observed under ultraviolet light. The fish was at large for 160 days. Tetracycline mark = m; annuli are indicated by the arrows.

greater amberjack were fitted to the von Bertalanffy growth model (Fig. 7). Because there was no difference between male and female models ($P > \chi^2 = 0.496$), data were combined and resulted in

$$L_t = 138.9(1 - e^{-0.25(t + 0.79)}). \qquad (r^2 = 0.96, n = 552)$$

Tag-recapture data obtained from the CGTP yielded 25 data points useful for comparison of growth rates, and an additional six data points from our mark-recapture experiment. Predicted lengths fell along the trajectory of a line where predicted lengths equalled observed lengths (Fig. 7). The differences between observed and predicted values were both positive and negative. There was a tendency to under-predict fish size above 80 cm recapture length. The growth of tagged and recaptured fish provided additional support of our age estimation technique.

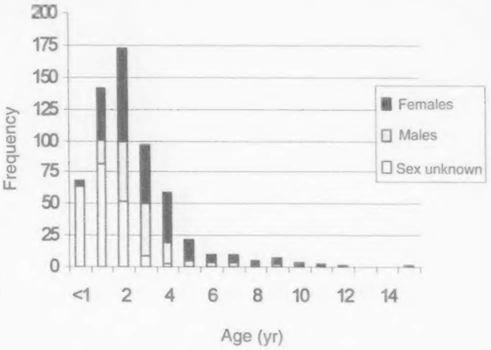

Figure 5

Estimated age-frequency histogram, identified by sex, of northern Gulf of Mexico greater amberjack collected from April 1989 to June 1992.

Discussion

Our observations of sex-related differences in maximum size of greater amberjack are consistent with the findings of previous investigators. Burch (1979) reported a maximum size of 145.0 cm for males and of 155.5 cm for females and noted that the mean fork length of females was greater than that of males of the same age. Humphreys (1986) reported a maximum size of 106.0 cm for males and of 149.4 cm for females. We found that the maximum size of males (132.7 cm) was less than that of females (144.1 cm) and that females represented 72% of the fish over

100 cm. Our data support the hypotheses that the maximum size in greater amberjack is sex related. Similar results were reported for other pelagic species (Atlantic and Pacific blue marlin, and swordfish) suggesting that females either grow faster, live longer, or both (Wilson, 1984; Wilson et al., 1991).

Charterboat-caught greater amberjack were collected year-round from the Louisiana coast, providing us with the opportunities to examine seasonal changes in the population. Size-frequency analysis of these data showed that fish were largest from May to September and smallest from November to February, suggesting a seasonal shift in the size frequency of individuals in the population off Louisiana. Although this seasonal size difference could be due to sampling bias, we believe that greater amberjack have an affinity for warmer waters and that the cooler waters associated with winter initiate an emigration from Louisiana waters. Burch (1979) reported greater amberjack migrating southward from December to May and northward from June to December in Florida. Baxter (1960) reported a northward migration of California yellowtail (as *Seriola dorsalis*) off California waters during early spring. The size at which greater amberjack begin to migrate is not known (Burch, 1979).

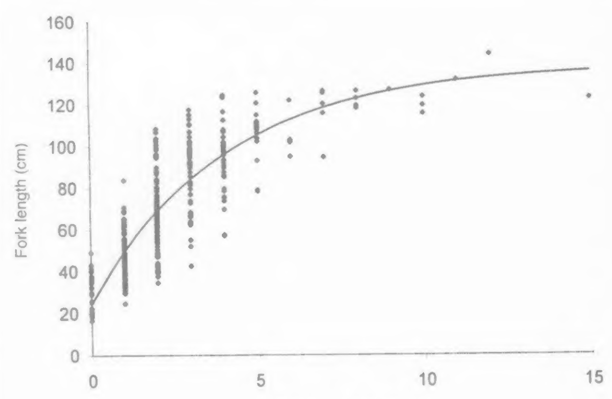

Figure 6

Plot of the estimated age and length of north-central Gulf of Mexico greater amberjack and the resultant von Bertalanffy relationship.

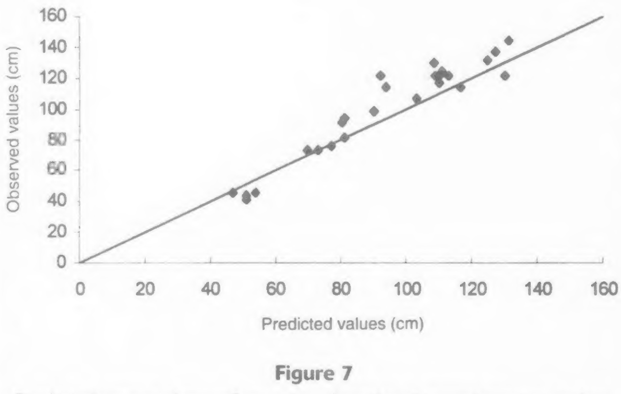

Figure 7

Predicted versus observed recapture lengths of tagged greater amberjack. Predicted values were calculated by using our von Bertalanffy growth parameters. The solid line covers points where the predicted and observed values are equal.

Females tended to be more abundant than males throughout our study, although the female-to-male ratio varied with time of year and source. This is contrary to Burch (1979) who reported female-to-male ratios from 0.6:1 to 2:1 with males more numerous in all months except July, August, and September. Humphreys (1986) reported a female-to-male ratio of 0.9:1. In our study, no trend in sex ratio was detected for charterboat-caught greater amberjack, and the overall ratio was 2.5:1. It is possible that males are more abundant off the west coast of Florida and females are more abundant off Louisiana. Thompson et al.[1] found that male cobia (*Rachycentron canadum*) dominated in the west-central Gulf of Mexico, whereas females dominated in the east-central Gulf of Mexico.

Otoliths

Greater amberjack otoliths are small, fragile, and complex in shape. In a comparison of external and internal features with those of other pelagic species, sagittae were found to be similar in shape to those of red steenbras (*Petrus rupestris*) (Smale and Punt, 1991), tunas (C.A. Wilson, unpubl. data), billfishes (Wilson et al., 1991), and several other carangids (*Alectis, Caranx, Chloroscommbrus, Elegatis*, and *Uraspis*, senior author, unpubl. data)

We tried several models (power function, logistic equation, Gompertz and Richards models) to describe the relationship between fish size (fork length) and otolith size (sagittal weight). A negative exponential in the form of the von Bertalanffy equation provided the best fit (r^2=0.96) and indicated that sagittal weight continues to increase even after increases in fish length or weight slows or ceases (Pawson, 1990). This finding provides further evidence that otolith growth is more closely associated with time than with fish size as the fish becomes older. Secor and Dean (1989) suggested that otolith growth was a function of both somatic growth and time in young fish. We propose that as fish grow and approach an asymptotic size, otolith growth continues at a basal level and does not reach an asymptote. This is further evidence of the disassociation of otolith growth and fish growth in older fish. Continued sagittal growth throughout the life of the fish is the property that makes sagittae a useful ageing tool (Gamboa, 1991; Casselman, 1990).

Opaque zones (annuli) observed in transverse sections of greater amberjack sagittae were not as consistent as those reported in other species such as the sciaenids (Beckman, 1989; Casselman, 1990). Wilson et al. (1991) found that establishment of annual patterns in transverse sections of sagittae from pelagic fishes was best accomplished through interpretation of a combination of growth features on the surface of and in sectioned sagittae. Transverse sections of greater amberjack sagittae contained growth features described by Smale and Punt (1991) for red steenbras and by Wilson (1984) and Prince et al. (1986) for billfishes. We used similar criteria for discrimination of annual patterns in transverse sections of greater amberjack sagittae. Our criteria included external ridges on the lateral side of the sagittae, ridges within the sulcus acousticus, internal opaque and translucent zones, and the association of these features with a common area where many growth bands converged (Fig. 3A). All these growth features were coincident with annuli that were validated by using oxytetracycline-injected fish (Fig. 4). Smale and Punt (1991) found similar patterns in transverse sections of sagittae from red steenbras (*Petrus rupestris*). Although they reported fish as old as 25 years, transverse sections of sagittae from red steenbras looked similar to those of greater amberjack.

Disagreement over age estimates based on the above criteria was usually over an assignment of the first annulus. In some specimens a prominent opaque zone occurred adjacent to the core; we concluded it was laid down during the first winter and therefore did not consider it an annulus. Baxter (1960) reported that the first annulus was formed on the scales of yellowtail (as *Seriola dorsalis*) during their second winter, which was 18 months after hatching. We considered the first annulus in amberjack to be that which was laid down in the second year, when fish were actually 15 to 21 months old. When corrected for the discrepancy of the first annulus, the coefficient of variation and index of precision for the two readers were 0.15 and 0.11, indicating reasonable consistency in annulus interpretation. Similar values were reported by Wilson et al. (1991) for Atlantic blue marlin.

Apparently the sex-related size difference in amberjack is due to age-related differential mortality. Most of the greater amberjack collected were under 5 years old, although we found fish as old as 15 years. Males ranged from 1 to 9 and females ranged from 1 to 15 years. Females represented 76% of the samples above age 7. Burch (1979) found female greater amberjack to age 10 and males to age 8 for fish taken by southern Florida charterboat fishermen. The only other pelagic predator that demonstrates age-related sexual dimorphism, where females outlive males, is swordfish (Wilson and Dean, 1983). Greater amberjack also share a life history similar to both great barracuda and cobia in that they are all moderately long-lived pelagic reef species, and greater amberjack could be expected to exhibit similar patterns of longevity for males and females. However, deSylva (1963) found no age difference between sexes for great barracuda (*Sphyraena barracuda*). Richards (1967) reported no sex-related age differences for cobia (*Rachycentron canadum*) from mid-Atlantic waters, and Thompson et al.[1] reported similar findings for cobia from the Gulf of Mexico. We conclude that greater amberjack males die at a younger age than do females. More research is needed to determine whether these differences are real or are the result of sampling biases used in our study.

The relation between sagittal weight and age demonstrated that otolith weight can be used to estimate relative age. This finding is consistent with that for other pelagic species (Wilson, 1984; Wilson et al., 1991). Sagittal weight can provide a useful management tool because the random sampling and weighing of greater amberjack sagittae can be used to estimate age without the additional time and cost required for sectioning. We used a negative exponential to model the relationship between otolith size and fish size. The fit of this model indicates that otolith size continues to increase over time.

Growth

The von Bertalanffy growth parameter estimates obtained in our study were similar to both Burch's (1979) and Humphreys' (1986). Like Humphreys (1986), we did not find differences by sex. Burch (1979) reported L_∞ of 146.3 cm, 159.7 cm, and 164.3 cm for males, females, and sexes combined for charterboat- caught greater amberjack in Florida waters. Humphreys (1986) reported L_∞ of 149.3 for Hawaiian greater amberjack (sexes combined). We obtained an L_∞ of 138.8 cm, slightly smaller than that obtained by other authors; differences may be due to duration of the growing season, because greater amberjack studied by other authors came from warmer climates where growth may have been more rapid. Our comparison of observed recapture lengths with predicted recapture lengths (Fig. 7) further verified our age-estimation technique. Of interest was our observation that this method tended to underestimate fish size at sizes larger than 80 cm. Because most of the tagged fish were collected off south Florida, it is possible that they grow slightly faster than those off Louisiana.

Conclusion

Our analysis provides evidence that greater amberjack from the north-central Gulf of Mexico are moderately long-lived, living up to 15 years. They demonstrate a sexual dimorphism, where females grow larger than males, but this appears to be age related because males die younger. Our use of sagittal annuli is validated for only two- and three-year-old fish and future studies will be needed to complete age validation.

Acknowledgments

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Mercury levels in four species of sharks from the Atlantic coast of Florida

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Florida's commercial and recreational shark landings represent a significant portion of the total U.S. Atlantic shark landings (NMFS, 1993). Shark landings have increased significantly during the past decade because human consumption of shark meat has become increasingly acceptable and because, in Asian markets, the demand for shark fins is very high—as are the prices paid for them (NMFS, 1993; Brown, in press). The east-central coast of Florida is an important area for commercial and recreational shark fishing, and a wide array of shark species, including those examined in this study, are landed in this region (Trent et al., 1997; FDEP[1]).

Mercury, a toxic metallic element, has been shown to bioaccumulate in fish tissue, and therefore, fish can represent a major dietary source of mercury to humans (Phillips and Buhler, 1978; Turner et al., 1980; Lyle, 1986). Methylmercury is the most toxic form of mercury for humans to consume (Meaburn, 1978; NMFS, 1993) and essentially all mercury found in fish muscle tissue (>95%) is in the monomethyl form (CH_3Hg)(Grieb et al., 1990; Bloom, 1992). Therefore, the measurement of total mercury provides an approximation of methylmercury and has been recommended as the standard for regulatory monitoring (Bloom, 1992). Elevated mercury concentrations in fish have been a growing concern among resource management agencies. Apex predators, particularly long-lived species such as billfishes (Förstner and Wittman, 1981; Barber and Whaling, 1983; Kai et al., 1987), tunas (Miller et al., 1972), mackerels (Meaburn, 1978), and sharks (Forrester et al., 1972; Walker, 1976; Lyle, 1986; Vas, 1991; Hueter et al., 1995, and others) have been reported to accumulate relatively high levels of mercury.

In May 1991, the Florida Department of Health and Rehabilitative Services (FHRS) released a health advisory urging limited consumption of all shark species from Florida waters.[2] Owing to mercury concentrations in excess of U.S. Food and Drug Administration and State of Florida standards, FHRS recommended "adults should eat shark no more than once a week; children and women of childbearing age should eat shark no more than once a month." State of Florida guidelines recommended that fish containing less than 0.5 ppm of total mercury should represent no dietary risk, fish containing 0.5 to 1.5 ppm of total mercury should be consumed in limited amounts, and fish containing greater than 1.5 ppm of total mercury should not be consumed. The 1991 health advisory regarding sharks in Florida waters was derived from a limited number of samples taken from retail sources and from studies that lacked important information regarding species, capture location, sex, and size of sharks examined. Increased landings of sharks in Florida for human consumption (Brown, in press; FDEP[1]) has prompted the need for more detailed information regarding mercury levels in Florida shark species.

Consequently, we report here analyses of total mercury levels in the muscle tissue of three carcharhinids (bull shark, *Carcharhinus leucas*; blacktip shark, *C. limbatus*; and Atlantic sharpnose shark, *Rhizoprionodon terraenovae*) and one sphyrnid (bonnethead shark, *Sphyrna tiburo*) from the east-central coast of Florida.

Materials and methods

Sample collection and mercury analysis

Sharks were collected during the Florida Department of Environmental Protection, Florida Marine Research Institute's Fisheries-Independent Monitoring Program in the Indian River Lagoon system and adjacent coastal waters or from commercial gillnet or longline fisheries operating in the nearshore

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[1] FDEP (Florida Department of Environmental Protection) Marine Fisheries Information System, Fisheries Assessment Section, 100 Eighth Ave. SE, St. Petersburg, FL 33701.

[2] FHRS (Florida Department of Health and Rehabilitative Services). 1991. Health Advisory for Marine Fish. 1317 Winewood Blvd., Tallahassee, FL 32399, 3 p.

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and offshore waters of east-central Florida. All bull sharks were collected from estuarine nursery habitats within the Indian River Lagoon system from Oak Hill, Florida (approximately 28°52'N), south to the Ft. Pierce Inlet area (approximately 27°28'N). All blacktip, sharpnose, and bonnethead sharks were collected in nearshore and offshore waters from northern Cape Canaveral, Florida (approximately 28°55'N), south to the Sebastian Inlet/Wabasso, Florida, area (approximately 27°45'N). Samples were collected from 1992 to 1995.

Sharks were placed directly on ice and returned to the laboratory, where species, precaudal length (PCL), and sex were recorded. Stage of maturity was determined by examination of internal and external reproductive organs, as well as by comparison of shark size with estimates of size at birth or maturity from previous studies (Parsons, 1983, 1993; Branstetter and Stiles, 1987; Castro, 1996). Individuals were classified as neonates on the basis of unhealed or healing umbilical scars (Castro, 1993). To allow for comparisons with other studies, total length (TL), fork length (FL), and other morphometrics were also recorded according to Compagno (1984). With the exception of embryos, all sharks sampled were considered to be within the size range landed in Florida recreational or commercial fisheries. Axial muscle tissue samples were removed from the left dorsal area anterior to the origin of the first dorsal fin. White muscle tissue taken from this region is representative of the portion of shark used for human consumption. Tissue samples were immediately placed in sterile polypropylene vials, sealed, and frozen at –20°C until analyzed. Before analysis, tissue samples were digested by using standard procedures (EPA, 1991; Frick[3]) to convert all mercury in the sample to Hg^{+2}. The mercury in each digested sample was reduced to atomic mercury by reaction with excess stannous chloride. This atomic mercury was purged from solution in a gas-liquid separator and swept into an atomic absorption spectrometer for detection and quantification following standardized procedures (EPA, 1991; Booeshahgi et al.[4]) at the Florida Department of Environmental Protection's Division of Technical Services by using cold vapor atomic absorption spectrometry. Quality control measures included analysis of laboratory blanks, duplicate or triplicate tissue samples, and standard fish tissue reference material (DORM-1, obtained from the National Research Council of Canada) for each group of ten shark samples analyzed (EPA, 1991; Frick[3]; Booeshahgi et al.[4]). All mercury levels are reported as parts per million (ppm) wet weight.

Data analyses

Data regarding size and total mercury for each species were tested for normality by using the Kolmogorov-Smirnov test with Lilliefors' correction (Fox et al., 1994) and for homoscedasticity by using the F_{max}-test (Sokal and Rohlf, 1981) or by computing the Spearman rank correlation between the absolute values of the residuals and the observed value of the dependent variable (Fox et al., 1994). Linear regressions were used to describe relationships between shark size and total mercury concentration. Mercury data were log transformed to meet homoscedascity requirements. We used a *t*-test or Mann-Whitney rank sum test, as appropriate, to test for significant differences in total mercury levels and sizes between males and females for each species.

Results

Bull shark, *Carcharhinus leucas*

Eighty-three percent of 53 neonate and juvenile bull sharks (552–1075 mm PCL) tested from the Indian River Lagoon region had total mercury levels that were greater than or equal to the 0.5-ppm threshold level ($\bar{x}$=0.77 ppm; median=0.74 ppm; range 0.24–1.7 ppm) (Table 1). There was no significant difference between lengths of males ($\bar{x}$=735 mm PCL) and females ($\bar{x}$=754.6 mm PCL; *t*-test, $P>0.5$) nor was there a significant difference between mean total mercury levels between males and females ($\bar{x}$=0.76 ppm for both sexes; Mann-Whitney rank sum test, $P>0.05$). Ranges of total mercury for both sexes were also similar.

There was a significant positive correlation between total mercury level and bull shark length (both sexes combined) ($P<0.001$; Fig. 1). Total mercury levels in juvenile bull sharks increased as individuals grew larger, although some small sharks contained levels as high as those in larger sharks.

Blacktip shark, *Carcharhinus limbatus*

Total mercury levels for 21 juvenile and adult blacktip sharks examined ranged from 0.16 to 2.3 ppm

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[3] Frick, T. 1996. Digestion of fish tissue samples for total mercury analysis. Florida Department of Environmental Protection, Division of Technical Services, 2600 Blair Stone Road, Tallahassee, FL 32399. Report MT-015-1.

[4] Booeshahgi, F., M. Witt, and K. Cano. 1995. Analysis of total mercury in tissue by cold vapor atomic absorption. Florida Department of Environmental Protection, Division of Technical Services, 2600 Blair Stone Road, Tallahassee, FL 32399. Report MT-010-1.

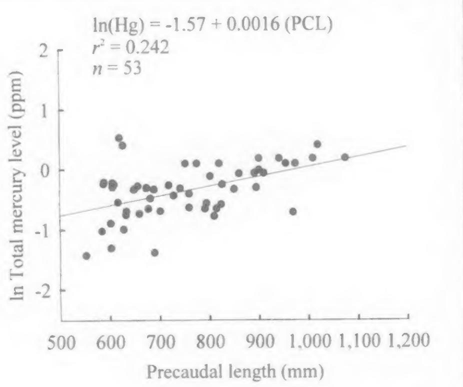

Figure 1

Relation between ln total mercury level (ppm) and precaudal length (mm) for juvenile bull sharks, *Carcharhinus leucas*, from the Atlantic coast of Florida.

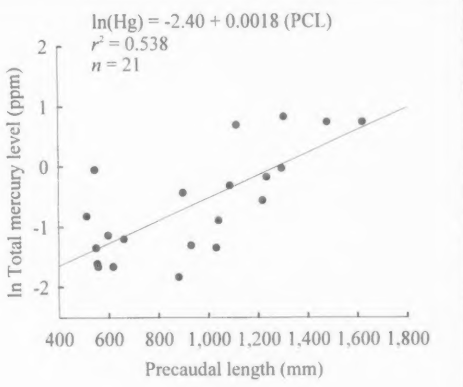

Figure 2

Relation between ln total mercury level (ppm) and precaudal length (mm) for juvenile and adult blacktip sharks, *Carcharhinus limbatus*, from the Atlantic coast of Florida.

Table 1

Total mercury levels in sharks from the Atlantic coast of Florida. n = number of sharks analyzed.

				Total mercury (ppm wet weight)			Precaudal length (mm)	
Species	Common name	n	Life history stage	Range	Mean	Standard deviation	Range	Mean
Carcharhinus leucas	bull shark	53	neonate/juvenile	0.24–1.7	0.77	0.32	552–1075	755.6
Carcharhinus limbatus	blacktip shark	21	juvenile/adult	0.16–2.3	0.77	0.71	513–1,623	939.6
		4	embryo	0.63–0.78	0.69	0.07	225–232	228.7
Rhizoprionodon terraenovae	Atlantic sharpnose shark	81	juvenile/adult	0.11–2.3	1.06	0.63	220–857	591.6
		6	embryo	0.17–0.29	0.22	0.02	74–85	80.3
Sphyrna tiburo	bonnethead shark	95	juvenile/adult	0.13–1.5	0.50	0.36	297–1081	590.3
		41	embryo	0.08–0.35	0.16	0.07	206–255	232.1

($\bar{x}$=0.77 ppm; median=0.44 ppm) (Table 1). Mean total mercury levels for females ($\bar{x}$=0.87 ppm) were higher than those for males ($\bar{x}$=0.58 ppm); however, these differences were not analyzed for statistical significance because sample sizes were small (n=14 females; n=7 males). The female blacktip sharks collected in this study were larger ($\bar{x}$=994.3 mm PCL) than the males ($\bar{x}$=830.1 mm PCL). Almost half (47.6%) of the blacktip sharks examined had mercury levels that were greater than or equal to the 0.5-ppm threshold level. The four blacktip shark embryos ($\bar{x}$=235 mm PCL), collected from a single 1050-mm-PCL female whose total mercury level was 2.3 ppm, had total mercury levels ranging from 0.63 to 0.78 ppm ($\bar{x}$=0.69 ppm; median=0.68 ppm) (Table 2). Mercury levels in these embryos equaled 27.4–33.9% of levels observed in their mother.

There was a significant positive correlation between total mercury level and blacktip shark length (both sexes combined)(P<0.0001; Fig. 2). Total mercury levels in blacktip sharks increased as individuals grew larger, although some small sharks contained levels as high as those in larger sharks.

Atlantic sharpnose shark, *Rhizoprionodon terraenovae*

Total mercury levels for 81 juvenile and adult Atlantic sharpnose sharks ranged from 0.11 to 2.3 ppm ($\bar{x}$=1.06 ppm; median=0.95 ppm) (Table 1). Although

Table 2

Total mercury levels of pregnant female sharks and associated embryos from the Atlantic coast of Florida.

	Pregnant female		Embryos		
Species	Precaudal length (mm)	Total mercury (ppm)	Precaudal length (mm)	Sex	Total mercury (ppm)
Carcharhinus limbatus	1050	2.3	230	M	0.78
			227	M	0.73
			235	M	0.63
			223	F	0.63
Rhizoprionodon terraenovae	766	1.9	84	F	0.29
			83	M	0.29
	782	1.6	76	M	0.17
			74	M	0.18
	784	2.3	85	F	0.19
			80	F	0.20
Sphyrna tiburo	990	1.1	229	M	0.12
			233	F	0.12
			236	F	0.14
	855	1	225	M	0.13
			237	F	0.19
			227	F	0.12
	1081	1.5	238	F	0.35
			230	M	0.14
Sphyrna tiburo	768	0.53	239	F	0.32
			229	F	0.30
			241	M	0.26
			224	F	0.28
			240	M	0.26
	877	1.1	238	F	0.11
			215	M	0.11
			228	M	0.13
			239	F	0.21
			230	M	0.10

females ($\bar{x}$=624 mm PCL) were significantly larger than males ($\bar{x}$=541.9 mm PCL) (*t*-test, $P<0.05$), total mercury levels of males ($\bar{x}$=0.92 ppm) and females ($\bar{x}$=1.15 ppm) were not significantly different (Mann-Whitney rank sum test, $P>0.1$). A total of 72.8% of all juvenile and adult Atlantic sharpnose sharks tested had mercury levels that were greater than or equal to the 0.5-ppm threshold level.

Total mercury levels for the six embryos (74–85 mm PCL) examined ranged from 0.17 to 0.29 ppm ($\bar{x}$=0.22 ppm; median=0.19 ppm). Mercury levels for embryos within each litter were very similar (Table 2) and equaled 8.3–15.3% of levels observed in their respective mothers. Overall mercury levels among litters were also similar (±0.02 SD). All confirmed pregnant females had levels greater than 1.0 ppm.

There was a significant positive correlation between total mercury level and Atlantic sharpnose shark length (both sexes combined)($P<0.0001$; Fig. 3). Total mercury level in this species increased as individuals grew larger. Total mercury levels for larger At-

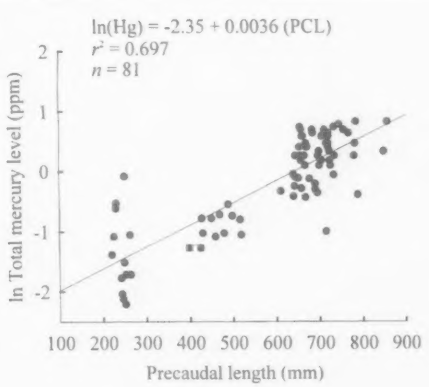

Figure 3

Relation between ln total mercury level (ppm) and precaudal length (mm) for juvenile and adult Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, from the Atlantic coast of Florida.

lantic sharpnose sharks (>500 mm PCL) were always greater than 0.5 ppm.

Bonnethead shark, *Sphyrna tiburo*

Total mercury levels for the 95 juvenile and adult bonnethead sharks sampled (297–1081 mm PCL) ranged from 0.13 to 1.5 ppm ($\bar{x}$=0.50 ppm; median=0.29 ppm) (Table 1). Forty percent of all juveniles and adults tested had mercury levels that were greater than or equal to the 0.5-ppm threshold level. Mean lengths of males ($\bar{x}$=564.6 mm PCL) and females ($\bar{x}$=619 mm PCL) were not significantly different (Mann-Whitney rank sum test, P>0.1) and there were no significant differences in mercury levels between males ($\bar{x}$=0.49 ppm) and females ($\bar{x}$= 0.50 ppm) (Mann-Whitney rank sum test, P>0.5). There was a significant positive correlation between total mercury level and bonnethead shark length (both sexes combined) (P<0.0001; Fig. 4).

Total mercury levels for the 41 embryos examined (206–255 mm PCL) ranged from 0.08 to 0.35 ppm ($\bar{x}$=0.16 ppm; median=0.13 ppm). Mean length for male and female embryos were both 232-mm PCL. Total mercury levels of male ($\bar{x}$=0.15 ppm) and female ($\bar{x}$=0.18 ppm) embryos were similar (Table 2). Mercury levels for embryos within each litter were similar (± 0.03 SD)(Table 2), as were overall mercury levels among litters (mean mercury level/litter = 0.1–0.28 ppm). Total mercury levels in embryos of this species equaled 9.1–60.4% of levels observed in their respective mothers.

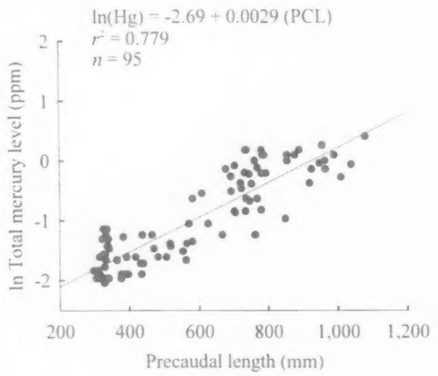

Figure 4

Relation between ln total mercury level (ppm) and precaudal length (mm) for juvenile and adult bonnethead sharks, *Sphyrna tiburo*, from the Atlantic coast of Florida.

Discussion

Results of this study indicated that most individuals in the four species of sharks tested had accumulated levels of total mercury that were as high as or higher than the regulatory threshold levels. Approximately 60% of the juvenile and adult sharks tested in this study had total mercury levels that were greater than or equal to the 0.5-ppm threshold level, and 12% had levels greater than 1.5 ppm. Information regarding mercury in sharks from other areas is limited; however, elevated levels of mercury in various shark species have been documented in several regions, including waters off Florida and the southeastern United States (Gardner et al., 1975; Hueter et al., 1995; FHRS[2]), Canada (Forrester et al., 1972), Great Britain (Vas, 1991), and Australia (Lyle, 1984, 1986). Although the life-history patterns of different shark species are diverse, most sharks grow slowly and have long lifespans. These general life-history characteristics, together with the high trophic status of many shark species, may contribute significantly to the accumulation of high concentrations of mercury (Lyle, 1984).

Mercury levels were directly related to shark size in all species tested. Length differences accounted for 78% of the total variation in mercury levels observed in bonnethead sharks, nearly 70% in Atlantic sharpnose sharks, and approximately 54% in blacktip sharks. The relation between mercury levels and length of juvenile bull sharks was less clear; length differences accounted for only 24% of the variation in mercury levels. The comparatively weak relation between mercury level and size in this species may stem from the fact that only neonates and small juveniles were sampled. Growth rates of bull sharks at the juvenile stage are thought to be quite variable (Dodrill, 1977; Thorson and Lacey, 1982; Branstetter and Stiles, 1987), which may explain some of the observed variability of mercury levels in juveniles of this species. For species we examined, the relations between total mercury and shark size demonstrated that larger, presumably older, individuals accumulated higher levels of mercury. The accumulation of mercury with increasing size and age is likely to be a result of the slow and inefficient elimination of mercury from fish tissue in relation to the rate of accumulation (Rodgers and Beamish, 1982; Bryan, 1984).

Because mercury levels increase as individuals grow larger, levels in juveniles can potentially be viewed as minima for the overall population. Although all bull sharks tested were either neonates or juveniles and the majority of blacktip sharks were juveniles or young adults, both species typically had high mercury concentrations. High mean methylmercury levels (>1.0 ppm wet weight) were also detected in 29 larger size-class bull sharks (approx. 1300–2800 mm TL) and six blacktip sharks (> approx. 1500–1800 mm TL) collected off Florida (Hueter et al., 1995). Two of these bull sharks were collected off east-central Florida; however, specific size or sex data were not reported for these individuals. The observed relation of length to total mercury in juvenile bull sharks, together with results reported for larger size-class bull sharks and other closely related species (Lyle, 1984, 1986; Hueter et al., 1995), indicates that large adult bull sharks could contain excessive mercury levels. Blacktip sharks collected off northern Australia, which were of similar mean length and size range to those examined in our study, also had relatively high total mercury levels (Lyle, 1984, 1986). These data suggest that through bioaccumulation, larger, older adults of these common species potentially contain excessive mercury burdens. Total mercury levels for larger size-class Atlantic sharpnose sharks (>500 mm PCL) that we examined were consistently greater than 0.5 ppm. Muscle tissue from the related Australian sharpnose shark, *Rhizoprionodon taylori*, and the milk shark, *R. acutus*, tested from northern Australian waters (Lyle, 1986) contained mercury levels that were comparable to levels we detected in Atlantic sharpnose sharks. Milk sharks of comparable size examined by Lyle (1986) had total mercury concentrations (range=0.16–2.00 ppm wet weight; $\bar{x}$=1.01 ppm) that were very similar to those in Atlantic sharpnose sharks in the current study.

Bonnethead sharks had the lowest mean mercury content of the four species tested. The relatively low levels found in bonnethead sharks may be related to the comparatively fast growth rate and short life span of this species; however, diet is also an important factor. Bonnethead sharks off Cape Canaveral, Florida (senior author, unpubl. data), as well as off southwest Florida (Cortes et al., 1996), feed principally on crustaceans, whereas the other three species consume a larger proportion of fish (Compagno, 1984; Snelson et al., 1984; Castro, 1996; senior author, unpubl. data). Although available data are limited, crustaceans may contain mercury levels that are lower than those found in many fish species (Gardner et al., 1975; Stickney et al., 1975; Jop et al., 1997).

Mercury levels observed in embryos and neonates, as well as comparisons between pregnant females and associated embryos, indicated that transmission of mercury from maternal sources may be an important factor contributing to total mercury concentrations in shark muscle tissue. Total mercury levels in embryos of all species examined ranged from 8.3 to 60.4% of levels observed in their mothers, whose mercury levels were greater than the 0.5-ppm threshold (Table 2). Mercury levels of embryos within all litters were found to be similar. Mercury concentrations in embryos were variable among species. Atlantic sharpnose and bonnethead shark embryos all contained total mercury levels below the 0.5-ppm threshold; in contrast, all four embryos collected from a 1050-mm-PCL female blacktip shark had mercury levels greater than the threshold level. Variations in mercury concentrations found in embryos of different species could stem from differences in gestation periods or related physiological differences. Blacktip sharks have a two-year reproductive cycle with a 12-month gestation period (Castro, 1996), whereas Atlantic sharpnose sharks have a one-year reproductive cycle with a 10–11 month gestation period (Parsons, 1983). Bonnethead sharks have a gestation period of only 4–5 months (Parsons, 1993)—the shortest known gestation period of any placental viviparous shark species (Parsons[5]). This short gestation period, combined with other physiological factors and maternal diet may explain why bonnethead shark embryos contained the lowest mean mercury levels in this study. Walker (1976) suggested that transfer of mercury to developing ova and embryos may reduce mercury levels in mature females; however, little is currently known about maternal transmission of mercury in fishes. Mercury levels were relatively high in large females despite transfer of mercury to developing ova and embryos.

Results of this study indicate that the majority of sharks examined accumulated levels of total mercury that were greater than or equal to the threshold level of 0.5 ppm determined by the state of Florida. Mercury concentrations in adults and larger juveniles were typically elevated for all species; however, relatively high concentrations were also frequently observed in smaller juvenile bull and blacktip sharks. These data support the current health advisory in Florida urging limited consumption of sharks because of elevated mercury concentrations. Our data, in conjunction with the results of other studies conducted in the region (Gardner et al., 1975; Hueter et al., 1995; FHRS[2]), illustrate that mercury concentrations in several commonly landed shark species from the southeastern United States often exceed state and federal regulatory levels.

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[5] Parsons, G. R. 1997. Department of Biology, University of Mississippi, University, MS 38677. Personal commun.

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A unique shell marker in juvenile, hatchery-reared individuals of the softshell clam, *Mya arenaria* L.

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The ability to identify individual bivalve mollusks in field populations is fundamental to understanding potential population regulatory mechanisms (such as the influence of population density, tidal height, and initial shell size on growth and survival rates, and fecundity schedules). Softshell clams, *Mya arenaria* L., have been commercially harvested from the soft-bottom intertidal zone in Maine since the mid-1800s and form the basis of an extensive fishery along its entire coast. Dramatic declines in landings during the past decade in Maine (Wallace, 1997), however, have resulted in attempts to use hatchery-reared juveniles to supplement wild stocks (Beal, 1994). In the past, distinguishing between cultured and wild bivalves in the field in order to follow their fate has been performed by using alizarin staining techniques (Newell and Hidu, 1982), by tagging individuals (Brousseau, 1979), or by applying colored marks (e.g. paint dots) to the valves (Peterson and Beal, 1989). Here, we describe a natural and unique shell marker for juvenile, hatchery-reared softshell clams that forms on the outer valves of individuals once they are placed in the field. The distinctive mark appearing on the surface of each valve obviates the need to apply physical tags to individuals and also eliminates the stress that small clams otherwise undergo when being tagged.

Methods

Clams were reared during the summer of 1983 at a 4-H clam hatchery in Jonesboro, Maine, and were held in running seawater in sediment-free trays at the Darling Marine Center, Walpole, Maine, until 25 May 1984. On that date, 5000 individuals (mean shell length $[\bar{x}_{SL} \pm 1\ \mathrm{SD}]=10.4 \pm 1.52$ mm; range= from 6.7 to 14.6 mm; $n=200$) were transported back to the Jonesboro hatchery where the clams were divided into five groups of 100, 200, 300, and 400 individuals (i.e. a total of 20 groups). All but ten individuals from each group (20 groups× 10 individuals=200 clams) were marked with a single, group-specific, color-coded dot (Mark-Tex Corp. paint) on both valves near the umbo. The remaining 200 clams were painted with two dots to ensure individual recognition and measured (greatest shell length) to the nearest 0.1 mm by using vernier calipers. Marking was performed at this time because it was not known whether a distinctive mark would form naturally on the surface of each valve once clams began adding new shell in the field. Clams were maintained overnight without seawater at the University of Maine at Machias in a walk-in cooler (ca. 5°C).

On 25 May 1984, a matrix consisting of two rows of ten 0.25-m^2 plots was established near the midtide level of an intertidal flat (the Narrows) located along the western shore of the Chandler River (44°39'04"N; 67°33'10"W) near the town of Jonesboro, Maine. Sediments consisted of poorly sorted muds with a graphic mean ±1 SD of $3.6 \pm 0.34\phi$ ($n=2$). The matrix was located approximately 55 m from the extreme high water mark and 35 m from the mean low water mark. Both rows were parallel to the shore and were spaced 1 m apart. Black rigid-mesh enclosures (DUPONT Vexar, 6.4 mm aperture), approximately 0.25 m^2 and 15-cm wide, were installed around each plot to restrict lateral movements of the small clams (Baptist, 1955). Because the enclosures had no mesh roofs, they allowed epibenthic and infaunal predators (*sensu* Commito and Ambrose, 1985) access to the clams (Peterson and Beal, 1989). The mesh of each enclosure wall was

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attached by staples to a 40 × 2.5 × 2.5 cm wooden stake at each corner. This square, fenced assembly was then pushed 8 to 10 cm into the sediments leaving a mesh wall projecting from 5 to 7 cm vertically.

Groups of clams were assigned randomly to the open enclosures on 26 May 1984. This completely random design resulted in five replicates of each of four evenly spaced planting densities ranging from 400 to 1600/m^2. The fate of the 200 clams marked with two dots is reported here (see Beal [1994] for results of increasing intraspecific density on the fate and growth of the remaining clams). To ensure that seagulls (*Larus* spp.) did not prey on the clams before they had the opportunity to burrow, one of us remained at the site until the tide had completely covered the clams and the enclosures. During this interval (ca. 2 hours) clams burrowed into the sediments approximately 20 minutes after planting. No clam was visible at the sediment surface at the time of tidal inundation.

Live and dead clams were recovered from each of the twenty open enclosures after 99 days (1 September 1984) by collecting the top 15 cm of sediment from each enclosure and sieving the sediment through a 0.5-mm mesh. For each live clam (marked with two dots or not), an obvious mark parallel to the entire shell circumference was visible on the shell at or near the size the animal was on 26 May 1984 (see "Results" section). This mark permitted us to estimate a shell growth index for every live clam:

$$\textit{Relative growth index} = [(\textit{final length} - \textit{initial length}) / \textit{initial length}] \times 100.$$

Index values greater than 100% indicate at least a doubling in growth.

Shells from this 1984 field experiment were not saved, but results from subsequent field trials in eastern Maine with hatchery-reared softshell clam juveniles (Beal, 1994) revealed that this shell mark remains visible for periods up to 1.5 years after planting. We used scanning electron microscopy (SEM) to describe the gross shell structure across the distinctive pre- and postplanting regions of the outer shell of juvenile, hatchery-reared clams. We used the valves of cultured clams (initial size similar to those reported above) that had been reared during 1989 at the Beals Island Regional Shellfish Hatchery (BIRSH), Beals, Maine, planted at the Narrows in May 1990 and recovered in October 1990. We also used SEM to examine the outer shell structure of wild juvenile clams (ca. 15 mm) taken from a nearby mudflat in Roque Bluffs, Maine, in September 1992.

Results

When viewed macroscopically, every live hatchery-reared clam taken on 1 September 1984 (regardless whether or not it had been marked with two dots) had a distinct line on its shell surface that appeared to correspond to its size at planting on 26 May 1984. Scanning electron microscopy (SEM) of the gross shell structure of wild juvenile clams (Fig. 1, A and B) revealed sharp ridges (=lines viewed macroscopically) approximately 15-microns apart punctuated by a relatively smooth region. In sharp contrast, the valves of cultured clams (Fig. 1, C and D) consistently revealed three distinct zones: an inner region from the umbo to a distinct area (line) of demarcation that was approximately 50-microns in width (Fig. 1D) and an outer zone from that line to the ventral margin. The inner zone was characterized by a pitted, amorphous surface with interrupted ridges, whereas the outer zone of the cultured clams (Fig. 1C) appeared similar to the entire surface of wild clams. Observations from experimental or stock enhancement outplantings of cultured clams from BIRSH in numerous coastal communities in Maine since 1987 indicate that the shell mark may be present for up to 1.5 years after planting (Beal, 1994).

To test whether the obvious line, or shell mark, could be used quantitatively to distinguish initial size at planting from subsequent shell growth, we examined closely the 57 surviving clams of the 200 that had been marked with two dots on 25 May 1984. We used calipers to estimate the initial size of the clam delimited by the obvious surficial shell mark (line). Next, we compared, for each clam, this estimate of initial (i.e. predicted) shell length with the one recorded on 25 May. If the hypothesis that the line is formed at or near the time of transplanting is correct, then the mean difference between actual (i.e. recorded) and estimated size should not be significantly different from zero. Results of a one-sample, two-tailed t-test demonstrated that the average difference was not significantly different from zero (−0.047 mm; t=−1.505; P=0.138; n=57). An alternative statistical approach is to plot the predicted initial shell length (y-axis) against the actual initial shell length (x-axis; Fig. 2) and to determine whether the straight line ($y = -0.229 + 1.017x$; r^2=0.97) is significantly different from the line $y = x$. The slope of the least squares equation for that line was not significantly different from unity (F=1.38; df=2, 55; P=0.26), and the intercept was not significantly different from zero (F=0.81; df=1, 55; P=0.37).

The mean relative growth index for the period 26 May to 1 September for the 57 marked survivors was 86.9 ± 2.26% SE (Fig. 3A). Mean final length of the same in-

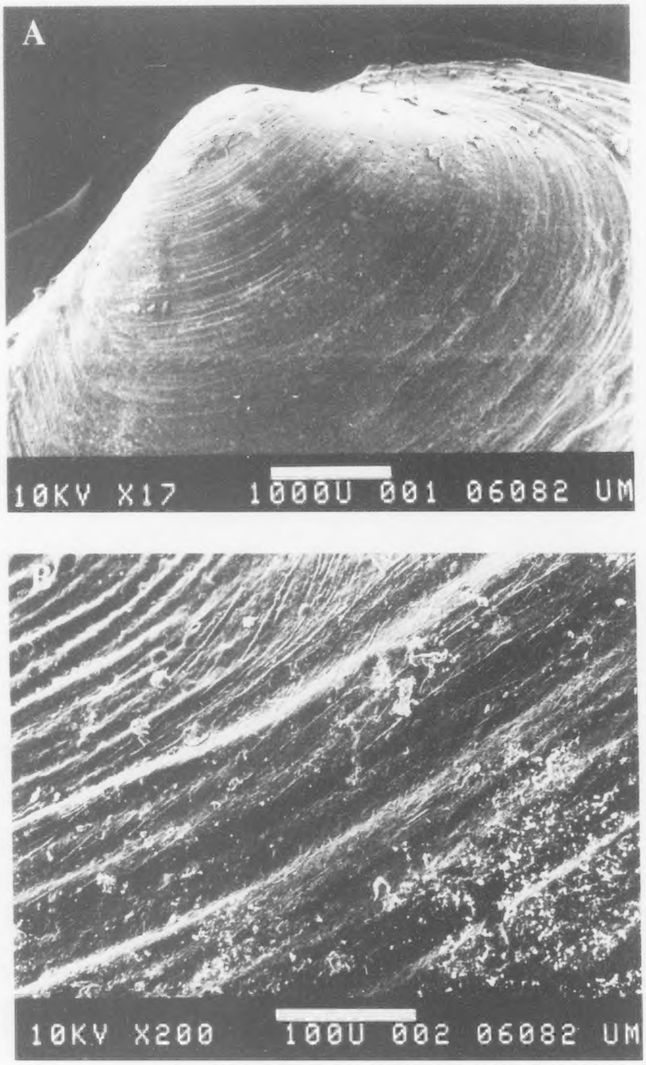

Figure 1

Scanning electron microscopy (SEM) of the shell surface of a wild (**A** and **B**) and cultured (**C** and **D**) juvenile softshell clam, *Mya arenaria* (length ca. 15 mm). The wild clam was sampled from a mudflat in Roque Bluffs, Maine, in September 1992. The cultured clam was reared at the Beals Island Regional Shellfish Hatchery and planted in May 1990, in a mudflat at the mouth of the Chandler River, near the town of Jonesboro, Maine. Photo B, taken near the umbo region of the wild clam, shows uninterrupted concentric ridges and a lack of pits and amorphous grooves. Photo C is an example of "the hatchery mark." It is a continuous, ca. 50–micron groove that extends along the ventral slope (anterior to posterior) of both valves and appears at that point on the shell surface associated with the time the animal leaves the hatchery and is placed in the soft-bottom benthos. Photo D, was taken along the anterior–posterior groove that appears at the interface before the period when new shell is deposited once the individual is transplanted to the field. The white bar indicates a length of 1000 μ for A and C and 100 μ for B and D.

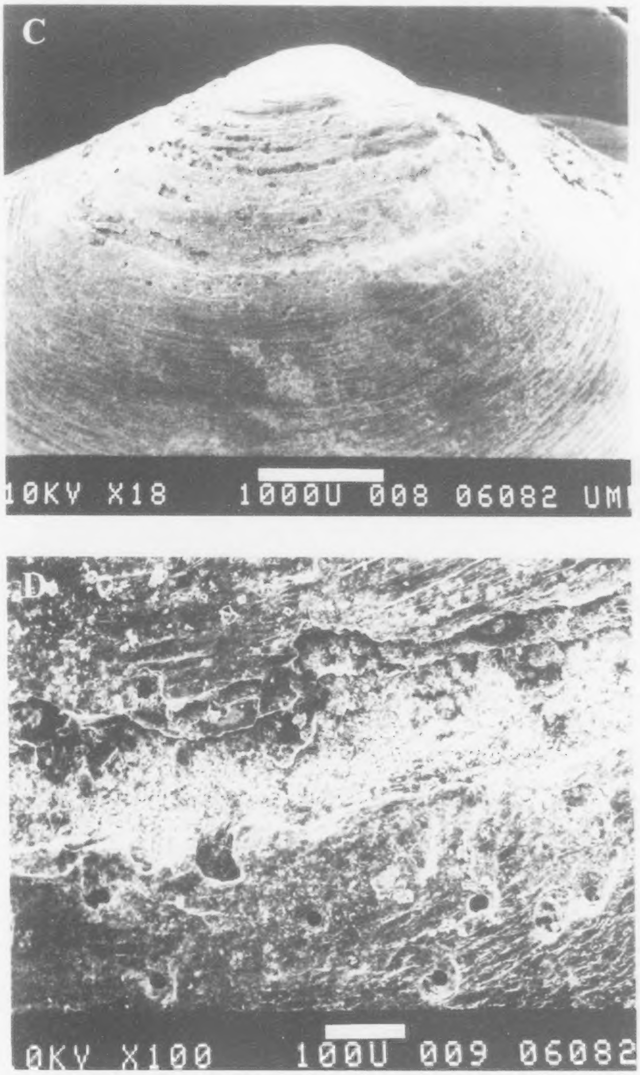

Figure 1 (continued)

dividuals was 19.6 ±0.24 mm SE (Fig. 3B), which equates to an average growth rate of 0.093 mm/day.

Discussion

Our data provide evidence of a distinctive mark or line being formed on the outer surface of the valves of juvenile hatchery-reared softshell clams. We have observed from other field tests and stock enhancement trials in Maine that the mark may be present for up to 1.5 years after planting, after which, the line disappears as the umbo region of the shell becomes increasingly worn, presumably on account of sediment abrasion from burrowing or seasonal repositioning (Zwarts and Wanink, 1989).

The formation of the line on the shell surface between the umbo and the ventral margin allows one to distinguish easily between wild and cultured juvenile clams and can be a valuable tool for resource

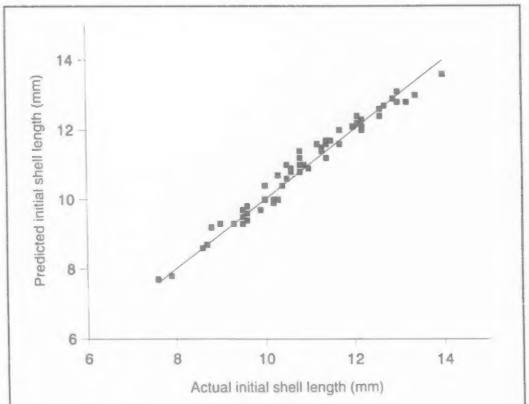

Figure 2

Predicted initial shell size versus actual initial shell size for the 57 hatchery-reared individuals of *Mya arenaria* marked with two dots that survived in open 0.25-m^2 field enclosures during the period from 26 May to 1 September 1984.

managers wishing to assess the fate of hatchery seed for stock enhancement purposes (Beal, 1994). In addition, it obviates the need to mark (physically or chemically) individuals or a group. If initially unmarked, juvenile, hatchery-reared softshell clams are planted in the field and examined within an 18-month period, the distinctive shell mark allows one 1) to determine initial planting size of individual hatchery-reared clams (Fig. 2); 2) to determine relative or absolute growth rates (Fig. 3, A and B); and 3) to estimate the time (e.g. season) when death occurred for those individuals that suffered mortality after planting. Similar disturbance lines were observed on juvenile, hatchery-reared northern quahogs, *Mercenaria mercenaria* (L.), planted from the laboratory to various subtidal and intertidal sites in North Carolina (Beal, 1983).

The origin of the shell mark may be related to conditions within the hatchery environment. After the field experiment described above, cultured softshell clam juveniles from BIRSH were planted in intertidal flats along the coast of Maine (1987–94) during the months of April through October for both manipulative tests and community-based stock enhancement efforts (Beal, 1994). In addition, cultured clam stock produced in a commercial shellfish hatchery (Mook Sea Farm, Inc., Walpole, Maine) were used in stock enhancement programs in Gloucester and Ipswich, Massachusetts (Whitten[1]). Regardless of hatchery origin, the same line appeared on the shells of all survivors planted in the soft-bottom intertidal zone at all locations, as well as on shells of those that grew before dying.

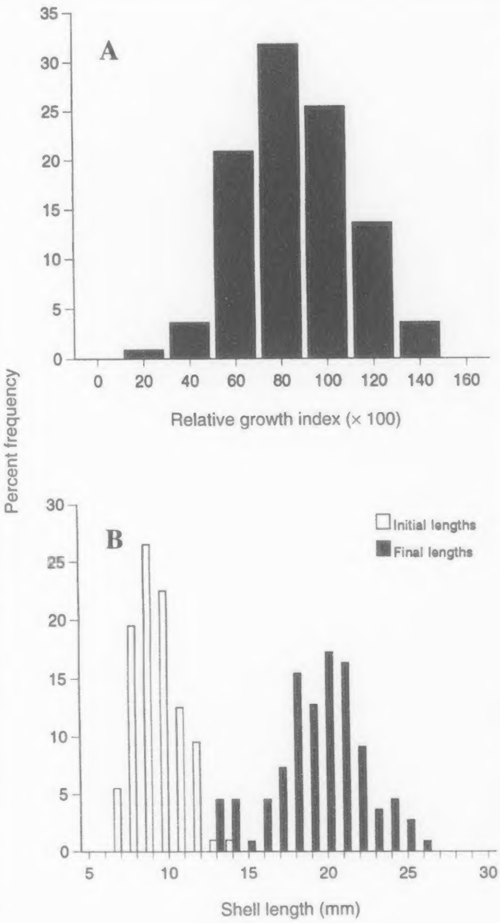

Figure 3

(**A**) Frequency distribution of relative growth rate index for the 57 hatchery-reared softshell clams marked with two dots (26 May to 1 September 1984). An index of 100% indicates a doubling of shell length. (**B**) Frequency distribution of initial (26 May 1984; n=200) and final shell lengths (1 September 1984; n=57) of hatchery-reared softshell clams.

The mark has been observed in clams planted at shell sizes as small as 3 mm and as large as 25 mm (Beal, 1994). In addition, this mark appears regardless whether clams are transplanted to the field directly from the hatchery or are overwintered in submerged, floating cages (*sensu* Beal et al., 1995) before transplanting to the field.

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[1] Whitten, J. 1996. Merrimak Valley Planning Commission, Haverhill, MA. Personal commun.

Although not specifically tested, at least two competing hypotheses may explain the mechanism that creates this shell marker. The first hypothesis is disturbance, for clams in the hatchery are grown in sediment-free trays with fine-mesh screening (150–1500 µ), handled (sieved) weekly, fed tropical species of microalgae such as *Isochrysis galbana* (Tahitian variety), and are grown at temperatures between 20 and 25°C—well above those normally experienced in the wild in eastern Maine. Once they have left the hatchery environment, clams are planted on flats and immediately burrow into sediments where 1) hatchery-produced disturbance ends, 2) the clams begin feeding on natural phytoplankton assemblages, and 3) they experience seawater temperatures that typically do not exceed 17°C. The new shell that grows is always distinctly whiter than the older shell. This difference in coloration may indicate a release from competition for calcium or aragonite which may be limited under hatchery conditions (Barber[2]). The second hypothesis is bacterial damage that may also relate to conditions in the hatchery where elevated levels of marine bacteria such as *Vibrio* spp. frequently occur. Qualitative tests for the presence of *Vibrio* spp. (using Difco TCBS agar [Elston et al., 1981]) at BIRSH are made regularly and show a general presence of these bacteria in the seawater within tanks holding juvenile clams, in the cultured algae, and on the valves of juvenile clams. These gram-negative, oxidase-positive, fermentive rods have been observed similarly in commercial bivalve hatcheries in the coastal northeastern United States (Elston, 1984) where they have been described as coating the shell surface of cultured juvenile northern quahogs, oysters, *Crassostrea virginica* (Gmelin), *Ostrea edulis* L., and bay scallops, *Argopecten irradians* (Lamarck). Bacteria in the family Vibrionaceae can erode and perforate areas on the surface of bivalve shells through the production of a variety of acidic metabolites that are inimical to normal deposition of calcium carbonate (Elston et al., 1982). The SEM photograph of the valve of the hatchery-reared softshell clam (Fig. 1, C and D) clearly shows pitting and amorphous grooves that may indicate a bacterial origin.

During the past decade, clam landings in eastern Maine have declined by nearly 75% (Wallace, 1997). Communities that manage their clam stocks in this and other regions along the coast are beginning to use cultured softshell clams to enhance clam production. Testing the biological and economic efficacy of hatch-and-release programs is critical for the development of sensible management programs. Results presented here demonstrate the ease of distinguishing cultured from wild *Mya* and will allow scientists as well as clam harvesters a rapid assessment of field planting programs.

Acknowledgments

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Occurrence of neonate and juvenile sandbar sharks, *Carcharhinus plumbeus*, in the northeastern Gulf of Mexico

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The sandbar shark, *Carcharhinus plumbeus*, is a large, coastal species of the western north Atlantic occurring from Cape Cod, Massachusetts, to Brazil, including the Gulf of Mexico and Caribbean (Bigelow and Schroeder, 1948; Springer, 1960). Sandbar sharks are targeted by commercial fisheries and account for up to 60% of the large coastal shark landings in U.S. southern waters (NMFS, 1993). Adults are highly migratory and mostly congregate offshore. Neonate and juvenile sandbar sharks, on the other hand, are commonly found in coastal nursery areas where they feed (Medved et al., 1985) and avoid predation (Springer, 1967; Branstetter, 1990) during summer months.

The presence of neonate and juvenile sandbar sharks has been well documented in coastal areas of the eastern United States. Springer (1960) reported juvenile sandbar sharks from Cape Cod, Massachusetts, to Cape Canaveral, Florida. Juvenile sandbar sharks are abundant in Chesapeake Bay and eastern shore of Virginia in less than 10 m (Medved and Marshall, 1981; Musick et al., 1993). Castro (1993) found neonate and juvenile sharks in Bulls Bay, South Carolina. Pratt and Merson[1] determined Delaware Bay, New Jersey, as a major nursery area for neonate and juvenile sharks. Further attempts to delineate the extent of nursery areas for sandbar sharks along the U.S. east coast continue (Damon, 1997; Pratt and Merson[1]).

Juveniles are not known to occur in coastal areas of the eastern Gulf of Mexico. The direct correlation of juvenile sandbar shark survivorship and future stock size (Cortés, in press) requires delineation of sandbar shark nursery areas. Thus, if recruitment to the stock is assumed to be entirely from sharks from the U.S. east coast, then underestimates of total population size could occur and affect overall stock assessments. This paper reports on the occurrence of neonate and juvenile sandbar sharks and the potential nursery area of these sharks in coastal waters of the northeastern Gulf of Mexico.

Materials and methods

Sandbar sharks were captured from October 1992 to October 1997 as part of studies on the distribution and abundance of sharks in the eastern Gulf of Mexico. Because sampling had various objectives, the variability in sampling design and methods precluded quantification of a valid time series of abundance (e.g. CPUE) from 1992 to 1997. In general, gill nets varied in height from 1.52 to 3.04 m and ranged in length from 30.4 to 273.6 m, and mesh sizes from 6.9 to 20.3 cm stretched mesh. Each net, regardless of size, was anchored at both ends and fished on the bottom. Longlines, which ranged in length from 76 to 335 m and consisted of 10–60 hooks, were anchored at both ends and fished so that one half fished the "midwater" and the other the "bottom." Gangions were 0.9–1.8 m long and hooks were size 3/0 and 12/0 (Mustad). Usually menhaden (*Brevoortia* spp.) was the bait of choice.

The nets or longlines, or both, were set over a 24-h period at various times. Gill nets and longlines were checked, or checked and pulled, and sharks were removed throughout each sampling period. Surface water temperature (°C), salinity (ppt), and light transmission (cm) were measured daily at each station.

After they were caught, sharks were sexed and measured (total length, TL) to the nearest mm. Sharks that were in poor condition were euthanized for life history information; those in good condition were tagged with a multirecapture, nylon-head, dart tag (Hueter and Manire[2]) and released. Sampling took place April to October of each year, occasionally from November to March.

Study area

Sampling sites were located in four major areas along the northeastern portion of the Gulf, Apalachee Bay to St. Andrews Bay, Florida (Fig. 1).

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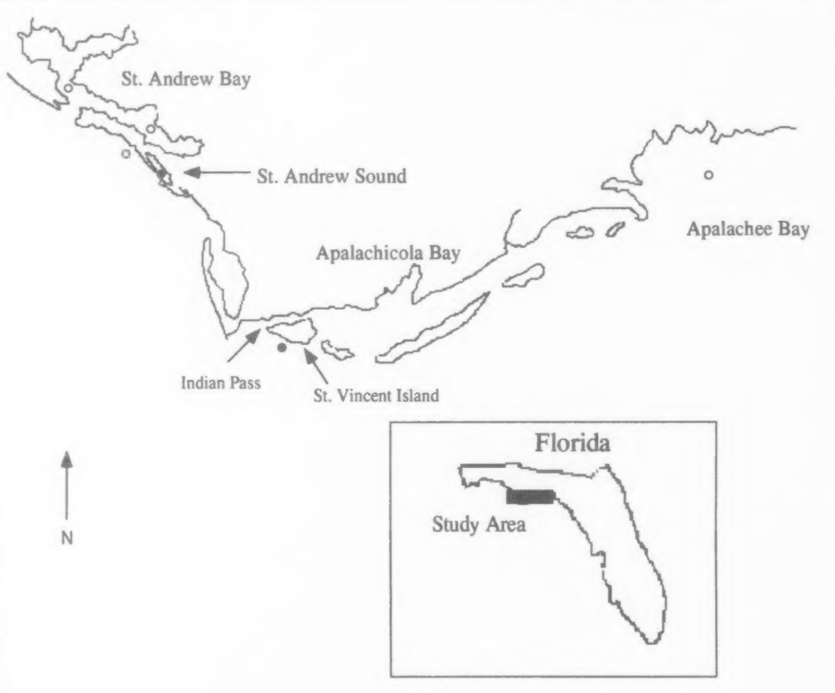

Figure 1

Map of the study area in northwest Florida near latitude 30°00'N and longitude 85°35'W illustrating the major sampling areas (○) and the two areas (●) in which sandbar sharks were captured from October 1992 to October 1997.

The eastern part of this area has an irregular coastline, few beaches and enclosed bay systems, and has large amounts of submergent (*Thalassia* spp. and *Halodule* spp.) and emergent vegetation (*Spartina* spp. and *Juncus* spp). The western part has numerous barrier islands and sand beaches and is composed of semi-enclosed bays. Tidal amplitude in the bays is highest in Apalachee Bay and generally decreases toward the west.

St. Andrew Bay consists of several embayments (average range 1.9–5.7 m deep) and has low freshwater inflow, low turbidities, and high percentages of sand in the substrate. Salinity ranges from 13 to 32 ppt and tidal amplitude averages 0.48 m. The system exchanges water with the Gulf of Mexico through two passes, a natural pass at the east end and a manmade pass at the west end.

St. Andrew Sound is a small semi-enclosed marine lagoon with expanses of submergent vegetation. It is about 14.5 km long and 0.2–2.0 km wide and has water depths from 3.5 to 4.5 m deep (mean high tide). Salinity ranges from 25 to 36 ppt and tidal amplitude averages 0.42 m. The sound exchanges water with the Gulf of Mexico through a pass (≈0.5–2.0 km wide) that was created near the center of Crooked Island by Hurricane Eloise in 1975.

Indian Pass is located at the western end of the Apalachicola Bay system. This area is about 2–3 km south of St. Vincent Island in the Gulf of Mexico where the average range of water depth is 5–10 m. The bay system surrounding this area is largely a line of barrier islands fronting the intersection of the Apalachicola delta and is the only bay system in Florida in which a large river system drains. As a result of river discharge, there is little submergent vegetation due to high turbidity. Salinity fluctuates from 15 to 35 ppt and tidal range is 0.66 m.

Apalachee Bay is an open ocean bay without barrier islands separating the area from the open Gulf of Mexico. The bay is broad, shallow (average 3 m), and extends about 15 km offshore. Salinity ranges from 22 to 36 ppt and tidal amplitude averages 1.0 m. Wave energy is low and the area has large expanses of submerged vegetation.

Results

Neonate and juvenile sandbar sharks (n=105) were captured in two areas of the northeastern Gulf of Mexico, Indian Pass, and St. Andrew Sound. Captured sandbar sharks were 572–1640 mm TL (Fig. 2). Seventeen were determined to be neonates and young-of-the-year (mean size=643 ±44.5 mm TL), as indicated by the presence of an open or partially healed umbilical scar. The largest sandbar shark with a partially healed umbilical scar was 720 mm TL. Following the age-length relationship provided in Sminkey and Musick (1995) and the life history stage classification in Cortés (in press) we estimated that 52 sharks were small juveniles (about 1–3 yr old), 34 were large juveniles (about 4–9 yr old), and 2 were subadults (about 10–12 yr old). Mature adults were not caught.

Sandbar sharks were captured in all years except 1995 (Fig. 3). The number of individuals collected was highest in 1993. Small juveniles were the dominant life stage captured in 1993 and 1997 and larger juveniles in 1994. Young-of-the-year, including neonates, were caught in all years sandbar sharks were captured.

The abundance and size of sharks varied with season (Fig. 4). Sandbar sharks were not captured until April when the water temperature approached 22°C. These were mostly small juveniles ranging in size from 800 to 1200 mm TL. Neonates were first captured in June when temperatures reached 25°C and young-of-the-year continued to be caught through October.

There was a significant relationship between abundance and water temperature (r^2=0.25, P=0.008), but not with salinity or turbidity ($P \geq 0.05$). Sandbar sharks were most abundant during summer months when all size classes were caught. Few larger juveniles were caught in fall.

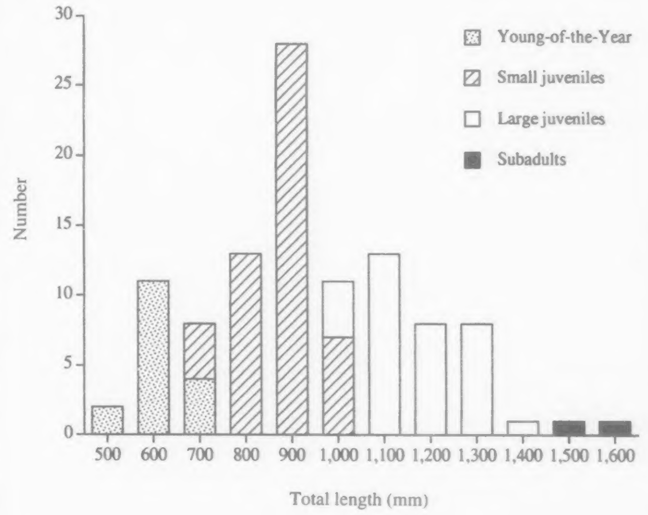

Figure 2

Length-frequency distribution of all sandbar sharks (n=105) by life history stage caught in gill nets and longlines from October 1992 to October 1997. Young-of-the-year includes neonates.

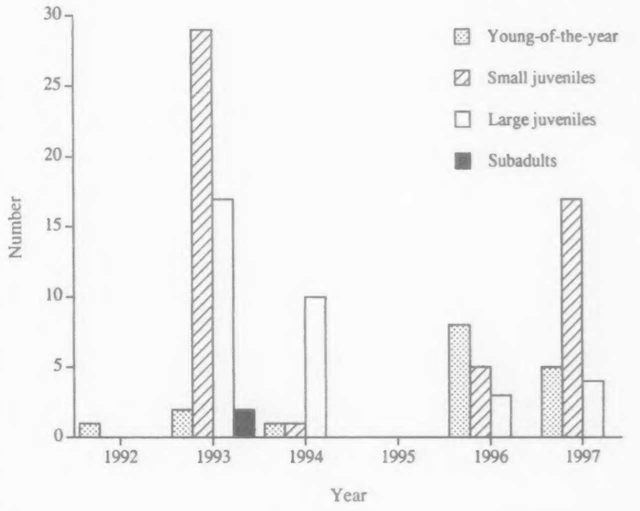

Figure 3

Overall abundance of sandbar sharks captured by year and life history stage from October 1992 to October 1997. Young-of-the-year includes neonates.

Discussion

Presence of neonate and juvenile sandbar sharks in the northeastern Gulf of Mexico suggests that sandbar sharks pup in the eastern Gulf of Mexico. Springer (1960) proposed the existence of two breeding populations of sandbar sharks, one off the mid-Atlantic coast

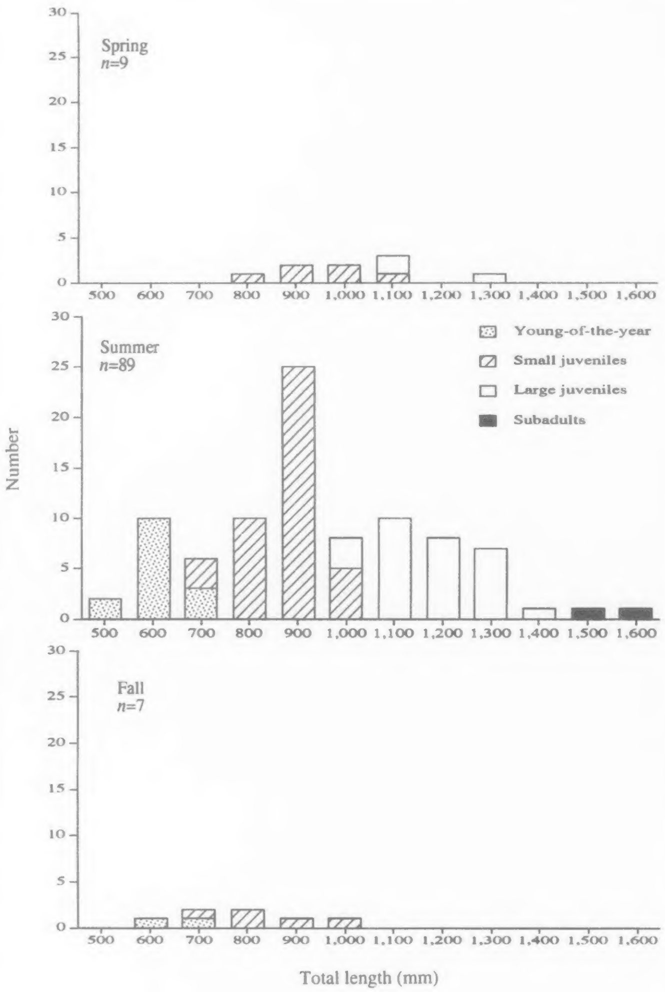

Figure 4

Length-frequency distribution of sandbar sharks by season and life history stage. Seasons were defined as spring (Mar–May), summer (Jun–Aug), and fall (Sep–Oct). Young-of-the-year includes neonates.

of the United States, one in the western Gulf of Mexico. Bigelow and Schroeder (1948) captured one sandbar shark that was 747 mm TL off the Texas coast, and Springer (1960) took a few females with full-term pups near the mouth of the Mississippi River. Branstetter (1987) captured two neonates (67 and 69 cm TL) from Galveston Bay, Texas. Some evidence of possible pupping areas in the eastern Gulf of Mexico was presented by Clark and von Schmidt (1965), who captured gravid females off Sarasota, Florida, and Branstetter (1981), who reported on six gravid females from a Shark Rodeo off Pensacola, Florida. However, no neonate or juvenile sharks have been previously reported from the eastern Gulf of Mexico.

Sandbar shark distribution in the northeastern Gulf of Mexico was limited to the mouth of the Apalachicola River, near St. Vincent Island; none were caught in three additional areas sampled and only two were captured in St. Andrew Sound. Although all areas sampled vary in environmental parameters, none of the environmental conditions measured appeared to be associated with the distribution of juvenile sandbar sharks. It is possible that sandbar sharks are attracted by the abundance of prey and bycatch from intense commercial shrimping operations that occur in the area surveyed at the mouth of the Apalachicola River.

The absence of gravid females in the survey does not preclude the presence of a pupping and nursery area. Females may be pupping farther inshore or offshore from the sampling area, at times when sampling did not occur or sampling gear may have had reduced efficiency at capturing larger sharks. Female sharks are reported to move into Chesapeake Bay to pup when water temperatures reach 18–20°C (Grubbs, 1996), and most sampling in this study began in April when water temperatures were usually above 20°C. In addition, mature female sandbar sharks are large (>1800 mm TL; Sminkey and Musick, 1995) and it is likely that they were able to avoid the sampling gear.

Neonate sandbar sharks (<age 1) usually reside in primary nursery areas where they were born through the first summer (Pratt and Merson[1]); thus it is unlikely that individuals captured in this area underwent significant migrations from another area. The paucity of tag and recapture information in the Gulf of Mexico also complicates understanding of the geographical and seasonal distribution of neonate and juvenile sandbar sharks. Future research should be focused on further delineation and annual monitoring of hypothesized nursery areas for sandbar sharks and on increasing ongoing tagging efforts.

Acknowledgments

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Different residence times of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, found in mixed aggregations over a seamount

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Aggregations of tuna can be found in association with seamounts throughout all the tropical oceans and these aggregations are often exploited by tuna fishing fleets (Fonteneau, 1991). In Hawaii, a fishery has developed over the last decade that targets the mixed species aggregations of predominantly subadult tuna found in association with the Cross Seamount located approximately 160 nmi south of Honolulu and Oahu and 150 miles east of South Point on the island of Hawaii (Fig. 1). Its shallowest depth is about 330 meters.

The Cross Seamount fishery is a hybrid troll, jig, and handline fishery that augments slow trolling methods by using frozen, cut and whole bait to induce feeding behavior around the fishing boat. Initially described as a yellowfin tuna (*Thunnus albacares*) fishery, closer scrutiny has revealed that the catch is dominated by juvenile bigeye tuna (*T. obesus*). Schools of skipjack tuna (*Katsuwonus pelamis*) are also found over the seamount but these are avoided by fishermen and, when skipjack tuna occur in mixed schools with the other species, the quite large size of the baits deters the capture of skipjack tuna. The fishery occurs year-round but fishing effort tends to subside periodically when larger tuna become available closer to shore—primarily during summer months.

Two concerns have arisen within the fishing community. First, fishermen exploiting the Cross Seamount resource were concerned that increasing fishing effort at the seamount by additional vessels entering the fishery would overexploit the schools of tuna associated with the seamount. Second, there was concern among the broader community that heavy fishing effort at the seamount might reduce the number of fish that were available to other gear types operating closer to shore. That is, the seamount might be a major "staging point" for fish that subsequently move into the coastal handline and troll fisheries. In response to these concerns, a tag-and-recapture program was conducted to elucidate the dynamics of the tuna populations associated with the seamount and to document the movements of individual fish forming those aggregations.

Materials and methods

Tag-and-release operations were conducted by trained tagging technicians placed onboard collaborating commercial vessels. Tuna were caught by crew members using handlines and pole-and-line methods, and the fish were then passed to the tagging technician for evaluation, identification, measurement, and tagging. Standard, serially numbered 11-cm nylon-tipped dart tags (Hallprint Pty, Australia) carried a message (stating a reward) and a toll-free phone number for reporting recaptured fish. Also, because the commercial fishing fleet in the seamount fishery consists of fewer than ten boats, close liaison was established with these boats to ensure maximum reporting of fish recaptured at the release site.

Residence times for tuna at the seamount were calculated by constructing tag-recapture attrition curves (Kleiber et al., 1987) that plotted the number of tagged fish recaptured against time at liberty. The elapsed time at which 50% of the releases had been recaptured at the point of release (Cross Seamount) represents the "half-life" of resident tuna within that area. That is, for a group of animals tagged at Cross Seamount, the residence time was defined as the elapsed time at which only half those animals remained at that location. In order to avoid disproportionate influence of fish recaptured immediately after release and be-

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Table 1

Fish tagged and released at Cross Seamount.

	Released at Cross	Recaptured at Cross		Recaptured elsewhere		Combined recaptures	
Yellowfin	458	86	(18.7%)	9	(1.9%)	95	(20.7%)
Bigeye	835	61	(7.3%)	12	(1.4%)	73	(8.7%)
Total	1293	147	(11.4%)	21	(1.6%)	168	(12.9%)

cause nighttime is when tuna often make significant horizontal movements away from their daytime haunts (Holland et al, 1990; Marsac et al., 1995), attrition curves were constructed only for fish recaptured for time at liberty >24 h.

Results

Between August 1995 and November 1996, 835 bigeye and 458 yellowfin tuna were released at Cross Seamount. The tagged bigeye tuna were between 40 and 105 cm FL; yellowfin released were between 40 and 90 cm FL. There were no significant differences between the two species in the size distribution of fish tagged and released (Fig. 2) or in size distribution of the recaptures. Because no effort was made to preferentially tag a particular species, the ratio of releases (65% bigeye, 35% yellowfin) reflected the ratio of species actually caught. Release and recapture data are summarized in Table 1.

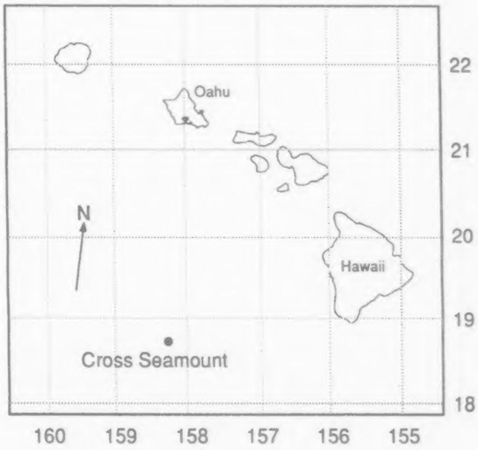

Figure 1

Chart of the study area showing position of Cross Seamount in relation to the main Hawaiian Islands.

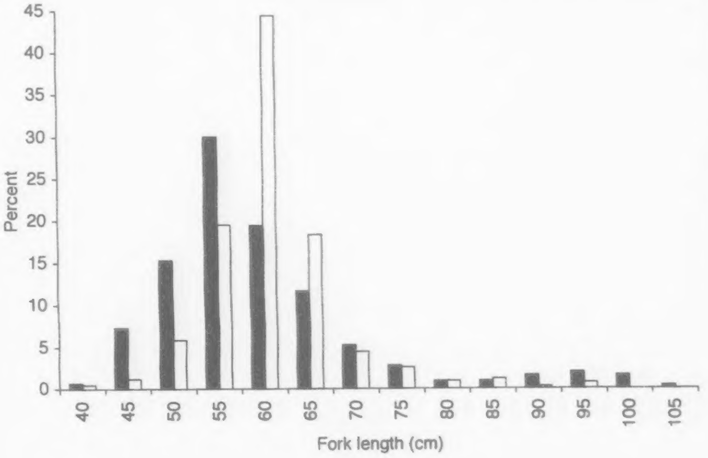

Figure 2

Size distribution of bigeye tuna and yellowfin tuna tagged and released at Cross Seamount. Solid bars = bigeye tuna; open bars = yellowfin tuna.

The numbers of yellowfin and bigeye tuna recaptured at Cross Seamount were aggregated into 30-day periods of time at liberty and plotted as percentages of total number of fish recaptured. The resultant regression curves for the recapture of each species are shown in Figure 3. An analysis of covariance indicated that the slopes of the attrition curves for the two species are significantly different (P=0.013). The attrition rate (slope of the regression line) for yellowfin tuna is approximately twice the rate for bigeye tuna, and the slopes indicate a residence time (50% recaptured) of 15 days for yellowfin tuna and 32 days for bigeye tuna. By contrast, the tag attrition curves for statewide returns (that is, time at liberty for all recaptured Cross Seamount yellowfin and bigeye tuna, regardless of recapture location) were not significantly different (*P*=0.45, Fig. 3).

In addition, there were more recaptures of bigeye tuna with longer periods at liberty than of yellowfin tuna at the seamount and the longest time at liberty was 169 days for bigeye tuna compared with the longest point-of-release recapture of 93 days for yellowfin tuna.

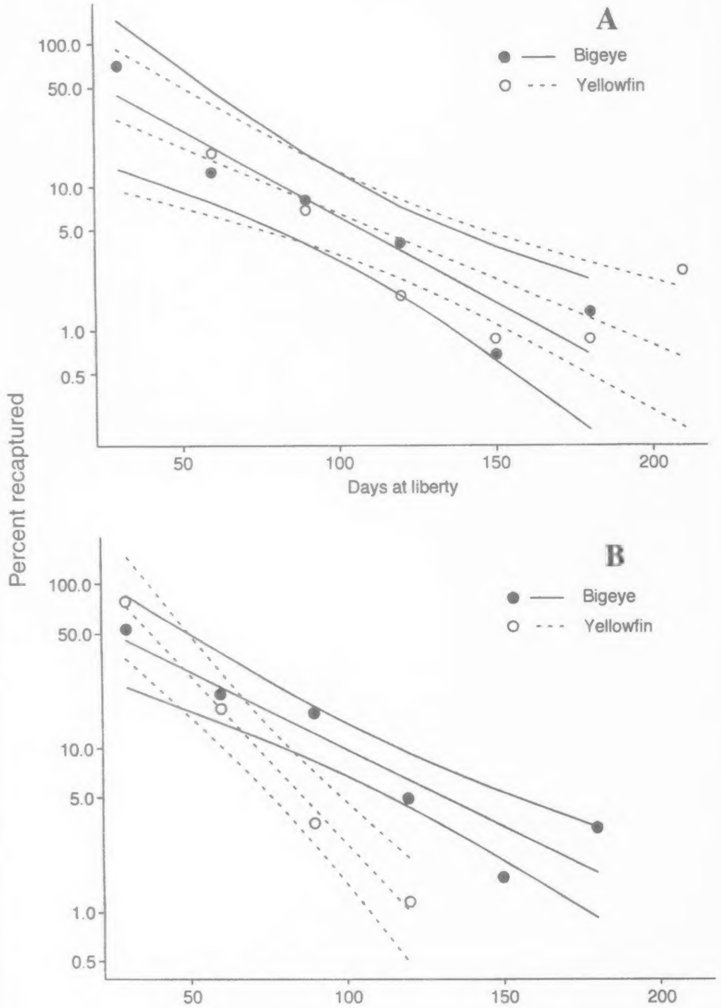

Figure 3

Tag recapture attrition curves (semi-log plots with 95% confidence contours) for bigeye and yellowfin tuna tagged and released at Cross Seamount. **(A)** All recaptures from all locations; **(B)** Recaptured at Cross Seamount.

Discussion

The main thrust of this analysis was to compare the residence times of the two tuna species at Cross Seamount. Consequently, many complicating factors often associated with analysis of tag-and-recapture data could be avoided (especially the impact of variability of fishing effort on the temporal pattern of recaptures) because effort could be assumed to be equal for both species. Therefore, the difference in the tag attrition curves, and the resultant difference in residence times ("half-life"), probably reflect real differences in the behavior of these two species at Cross Seamount. The similarity of the recapture curves for the entire area (Fig. 3) further suggests that methodological or experimental biases are not responsible for the differences in attrition curves obtained for these two species at Cross Seamount.

These results differ from those of Fonteneau (1991) who observed no differences in the temporal characteristics of recaptures of tagged bigeye, yellowfin, and skipjack tunas released at a seamount in the tropical Atlantic.

Fisheries data (Hanamoto, 1976, 1987) and acoustic tracking (Holland et al., 1990) both indicate that the open ocean behavior of bigeye and yellowfin tuna is different. Bigeye tuna select colder waters and are therefore usually found deeper than yellowfin tuna, which orient principally to the top of the thermocline and the mixed surface layer. However, this vertical separation breaks down around fish aggregating devices (FADs, Holland et al., 1990) and floating objects where bigeye tuna move closer to the surface and overlap in vertical distribution with yellowfin tuna. This same effect occurs at Cross Seamount where both species are caught in surface schools and bigeye tuna outnumber yellowfin tuna in the fishery. Similarly, mixed aggregations of yellowfin tuna, bigeye tuna, and skipjack tuna have been reported at seamounts in the Atlantic (Fonteneau, 1991).

Although the vertical behavior of yellowfin and bigeye tuna seems to merge at Cross Seamount, the current data indicate that the duration of horizontal orientation to the seamount (as measured by residence time ["half-life"]) is different.

The underlying advantage of seamounts to tuna biology is not well understood. Although seamounts can cause geographically stable regions of planktonic enrichment, it is not known if this enrichment persists long enough to move through the trophic chain to the level of the tuna forage base (Boehlert and Genin, 1987). We do know that Cross Seamount is situated in a very dynamic part of the ocean characterized by vortices created on the downcurrent side of the main Hawaiian islands (Flament et al.[1]). As these eddies spin off from the islands, current direction over the seamount can change frequently.

If an enriched area of prey does exist, and feeding is the principal underlying reason for tuna aggregations, it is difficult to understand why residence times are different for the two species and quite brief for both. The feeding advantage should impact both species equally and their residence times at the seamount should be similar. A comparison of the stomach contents of the two species when caught in seamount aggregations would be instructive. It is possible that, rather than acting as feeding stations, seamounts act as orientation points in the larger-scale movement patterns of these fish. Even though they may be too deep for visual detection, seamounts may be recognized by tuna through their ability to detect the effect of seamounts on the earth's magnetic field (Walker, 1984; Walker et al., 1984; Klimley et al., 1988). The seamounts may act as midocean reference points that may also occasionally harbor increased prey densities, the periodicity and persistence of which are driven by events in the surrounding oceanographic conditions.

A navigational role might explain why remote seamounts aggregate more tuna than seamounts located closer to land masses (Fonteneau, 1991) and why, in our study, the residence times were quite brief for both yellowfin and bigeye tuna species. The differences in the duration of orientation to the seamount might be explained if the navigational importance of seamounts is different in the broader behavioral repertoires of the two species.

Certainly, the current data indicate that Cross Seamount hosts transient populations of both tuna species rather than long-term populations. This brevity of residence at the seamount for both species probably reduces the chances of excessive fishing exploitation.

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Accuracy of at-sea commercial size grading of tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) in the Australian northern prawn fishery

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The size-frequency distribution of the commercial catch is often used as the basis of fisheries stock assessments (Pauly and Morgan, 1987; Gulland and Rosenberg, 1992) because most dynamic processes of populations (growth, survival, recruitment) are reflected in changes in this distribution. The data are generally collected, often at great expense, by sampling the catch at landing sites and markets, or onboard fishing vessels.

Size-frequency distributions of prawns (*Penaeus esculentus* and *P. semisulcatus*) can also be obtained from fish processors, who grade landings by size. These data are easier and cheaper to obtain than research samples, but unfortunately they are also considered less accurate and lack spatial information. However, they have been used in stock assessment of prawns in Kuwait (Jones and van Zalinge, 1981) and Malaysia (Simpson and Kong, 1978).

It is often difficult to relate size data obtained from a processor to time and place of capture of the prawns, but this is not the case when the product is packed onboard, as in Australia's northern prawn fishery (NPF).

Trawler operators in the NPF have voluntarily recorded size composition since 1985, when provision for this was made in operators' daily logbooks (between 30% and 45% of the tiger prawn catch reported in the logbooks contain size information). These books are therefore the most comprehensive source of information on the spatial and temporal size distribution of the commercial catch of the NPF. Present assessments of the fishery are based on deterministic growth and deterministic seasonal recruitment patterns (Wang and Die, 1996) and do not use size-structured data. If available, these data would help relax the assumption of deterministic recruitment and improve current stock assessments of the NPF.

Before the size data recorded in the logbooks can be used, however, the accuracy of size grading at sea needs to be assessed. This paper examines the accuracy of grading tiger prawns, by using data collected from a private firm, A. Raptis and Sons, that operates a large modern processing factory that regularly assesses the onboard grading of product purchased from NPF trawler operators.

Although the work presented here relates specifically to the NPF, the practice of onboard size grading is widespread in other fisheries around the world. Therefore our methods have potential application to other fisheries.

Methods

At-sea commercial grading procedures

Prawns landed from the NPF are size-graded at sea because both the demand and price structure differ for prawns of different sizes. Commercial sizes are based on the number of prawns of the same size per unit of weight (per pound), and the sizes are then grouped in a range to constitute a commercial grade. For example, "9 to 12 grade" means prawns in a range of sizes individually equivalent to between 9 and 12 per pound.

The size grades (especially for the larger sizes) used for tiger prawns are often more precise than those used for other species, and the grades selected by fishermen at sea vary with operator, pack size, and target market. For this project we examined the data for the two pack sizes that were most commonly used during 1993 and 1994: small packs (3 kg) and large, variable weight (12–15 kg) packs.

Small packs Since the early 1990s, the use of accurate digital scales on many vessels has improved the accuracy of procedures for packing prawns into 3-kg or smaller packs, as well as into more conventional larger packs. The sensitivity of

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these digital scales also makes it possible to pack in more precise grades of prawns.

Prawns for these small packs are initially sorted by eye by experienced crew, and many are verified by individual weighing. Those prawns that fall outside a particular size grade are removed and the remainder are graded according to corresponding count-per-unit-of-weight tables.

Large packs Prawns for onboard grading into the large packs are sorted by eye into groups of about the same size (occasionally by counting the number into a unit of weight [often a pound measured on analogue scales] and grouping them accordingly). Very large and very small prawns are removed and regraded.

Quality control assessment in the factory—source of data for analysis

A. Raptis and Sons process tiger prawns caught by their own large fleet of trawlers working in the NPF, as well as prawns purchased from other fishermen operating in the same area. The company randomly checks the quality of the packs entering its factory, including the accuracy of the grading.

Packs for quality-control assessment were selected at random for every vessel and from all consignments entering the factory. All packs were clearly marked with the vessel's name, the prawn species group, the grade of the prawns, and the date caught.

The selected samples were thawed individually. For the small packs, net weight was recorded, and size grading was checked by counting all prawns from each pack and averaging the count. Large and small prawns that did not fit the grade category were selected by eye, weighed, and graded individually, and the percentage by weight and the true grade of these prawns were recorded along with the percentage of those correctly graded.

With the large packs, a variable 2.5–3 kilogram sample of prawns was randomly taken from each pack, counted, and checked as above. The percentage by weight and the true grade of incorrectly graded prawns in the sample were recorded.

Categorical analysis

The results of all factory quality-control checks on both the small and large packs between mid-1993 and the end of 1994 were examined. Over this time, samples from 51 of the 127 boats that fished different areas in the NPF had been taken. We split the data into three time periods to find out whether the accuracy of grading early in the year differed from grading that took place later in the year when smaller prawns recruited to the fishery. Period one was from July to December 1993, period two from January to June 1994, and period three from July to December 1994.

Table 1

Commercial size grades (*) used in grading and quality-control assessments of tiger prawns for two different pack sizes. Also shown are the ranges of carapace lengths (mm) for each size grade.

Grade (prawn count (per lb)	Carapace length (mm)	Small pack	Large pack	Quality control
Under 6	>46	*	*	*
6 to 8	46–42	*	*	*
Under 10	>39		*	
9 to 12	41–36	*	*	*
10 to 15	38–33		*	
13 to 15	35–33	*	*	*
16 to 20	32–30	*	*	*
10 to 20	38–30		*	
Over 20	<29	*		
21 to 25	29–28		*	
26 to 30	27–26		*	
21 to 30	29–26		*	*

Data from the large packs, where the grades used were not the same as those for the small packs, were omitted from the analysis because they could not be compared directly. The commonly used size grades for both pack sizes are shown in Table 1, as well as the equivalent carapace length of the prawns.

The number of prawns (n) contained in the small packs was recovered by converting the net weight of the pack to pounds (weight in kilograms divided by 0.45359), and then by multiplying by the count-per-pound derived from the quality-control inspection. The number of misgraded prawns (r) in the small packs was estimated by multiplying the number of prawns in the sample by the percentage misgraded in that pack. The numbers misgraded for each period and each size grade were analyzed by fitting binary regression models by means of iterative weighted least squares. The number of misgraded prawns was assumed to have a binomial distribution:

$$Pr = \binom{n}{r} \pi^{r} (1-\pi)^{n-r}, \qquad (r=0, 1 \ldots n)$$

with $P(\text{misgraded}) = \pi$ and $P(\text{correctly graded}) = 1 - \pi$. The probability π was modelled in terms of the log-odds or logistic transformation $(\log(\pi/(1 - \pi))$. The computed deviance statistic, approximately distributed as chi-squared, was used in goodness-of-fit tests.

It was not possible to recover the total number of prawns in the large packs because the variable sample weight (between 2.5 and 3 kilograms) was not recorded in the Raptis database. Therefore estimates of the number of misgraded prawns were derived only for the samples and not for the whole pack. Because these samples were randomly chosen, it was possible to assume that the assessment of grading accuracy was representative of the grading accuracy for the whole pack.

For the large pack samples, the proportion misgraded had a mean (Eq. 1) and variance (Eq. 2) over the different samples

$$\text{Mean} = \pi \tag{1}$$

and

$$Variance = E\left(\frac{\pi(1-\pi)}{n}\right), \tag{2}$$

where π = the misgrading probability; and
n = the sample size.

Because the weight range of the samples was small, it was possible to estimate the expected reciprocal sample size

$$\left(E\left(\frac{1}{n}\right)\right)$$

(Eq. 4) by integrating over the sample weight range (assumed for mathematical convience to be uniformly distributed between 2.5 kg and 3 kg) (Eq. 3):

$$E\left(\frac{1}{n}\right) = \int_{2.5}^{3} \frac{0.45359}{\rho w} 2dw \tag{3}$$

$$= \left(\frac{0.45359 \times 2 \times \ln(3/2.5)}{\rho}\right) \tag{4}$$

where ρ = count per pound;
0.45359 kg = 1 lb; and
w = sample weight.

The relationship between Equations 1 and 2 here is the same as that for the binomial distribution; therefore the data were analyzed by fitting binomial regression models.

The size of misgraded prawns was examined to determine whether misgrading was a result of including small prawns in large grades or vice versa. The number of size grades in which misgrading occurred was also assessed.

Results

Small packs

Of the 21,443 tiger prawns in 293 small packs that were assessed, an estimated 1937 (9%) prawns in 229 packs were misgraded. There were significant changes in the proportion misgraded with both period of catch and size grade, with higher proportions of misgraded prawns in the small size grades (Table 2; Fig. 1A). Overall, grading accuracy tended to increase over the 18 months examined (Fig. 1A).

The size of the misgraded prawns over the different grades did not show a consistent pattern, but generally larger prawn grade packs tended to contain smaller prawns (Fig. 1A). The proportion of misgraded prawns that should have been in smaller grades, however, was

1. not constant over all size grades within each period of catch (Table 3; Fig. 1A);
2. not the same for each size grade over the three periods examined (Table 4; Fig. 1A).

Of the misgraded prawns, 99% were size-graded either one grade larger or one grade smaller. Only grades 9 to 12 and 16 to 20 contained prawns misgraded by as much as two size grades, with no more than 2% so misgraded. Because there was no larger grade, prawns misgraded in the under 6 size, were graded as 6 to 8.

If the proportion of prawns graded size i by fishermen at-sea that were actually size j (i, j=1 for under 6, 2 for 6 to 8, 3 for 9 to 12, 4 for 13 to 15, 5 for 16 to 20, and 6 for over 20 prawns per pound) obtained from the sample data are denoted by θ_{ij}, then the proportions, p_i, of all prawns graded as size i at-sea can be adjusted with the equation:

$$\sum_{i=1}^{5} p_i \theta_{ij} \tag{5}$$

to give a corrected grade size distribution (j=1, 2, ..., 6). Shown in Table 5 are the corrected distributions compared with at-sea grading for the small packs. The adjustments can be seen to be quite modest, and the at-sea gradings provide a reliable assessment of the size distribution.

Large packs

Samples containing an estimated 8210 tiger prawns from 124 large packs were assessed. Of these samples, an estimated 2914 (35%) prawns from 107 packs were misgraded. Again, there were significant

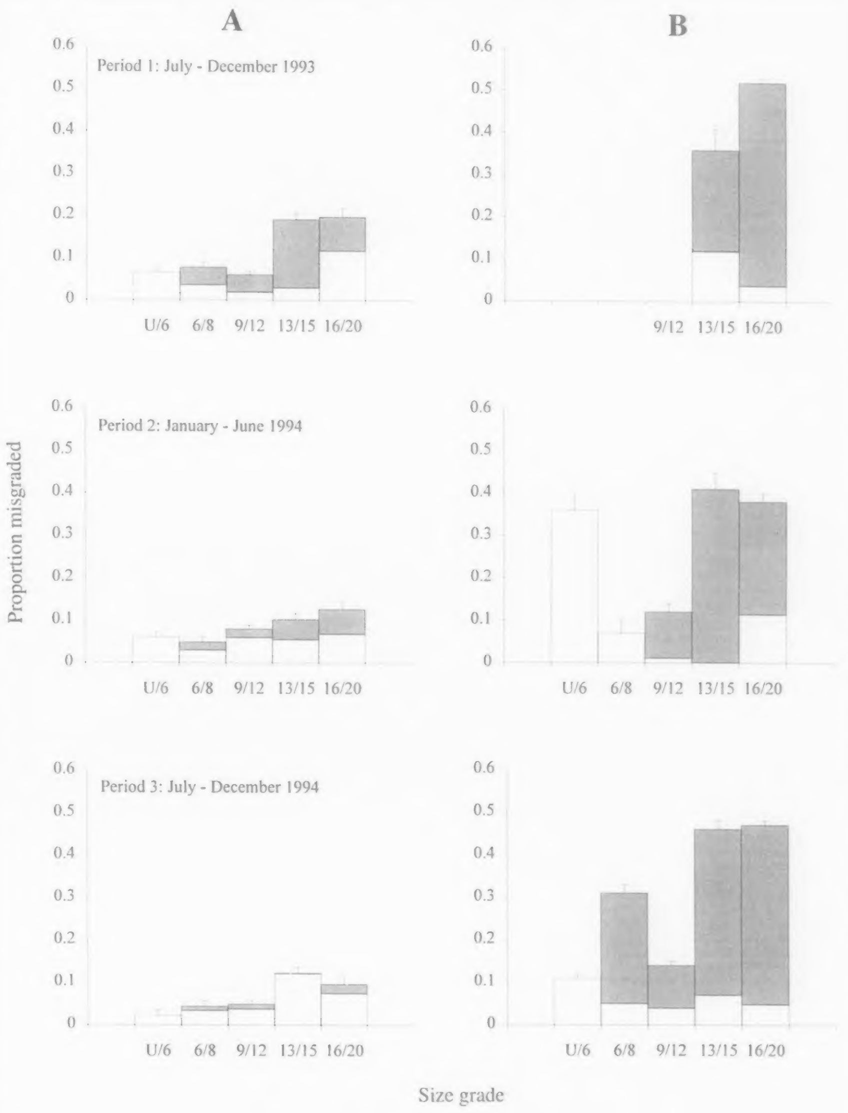

Figure 1

The proportion (+SE) of misgraded tiger prawns from each size grade, for (**A**) the small packs and (**B**) the large packs. The proportion misgraded was split between prawns that were misgraded too large (white) and those that were misgraded too small (gray).

changes in the proportion misgraded with period of catch and size grade, with significant differences in the proportion misgraded with period of catch, and generally higher proportions of the smaller size grades misgraded (Table 2; Fig. 1B).

There was a tendency for smaller-prawn grade packs to contain larger prawns (Fig. 1B). The proportion of misgraded prawns that should have been in a larger-size grade, however, was

1 not constant over all size grades, within any one period of catch (Table 3; Fig. 1B);

2 not the same for each size grade, over the three periods examined (Table 4; Fig. 1B).

Table 2

Binomial model fits for each period of catch (1: July–December 1993, 2: January–June 1994, and 3: July–December 1994) and pack-size combination. (a, b, c) denote groups of size grades with no significant differences in the proportion of misgraded prawns.

Pack size	Time period	Size grade Under 6	 6 to 8	 9 to 12	 13 to 15	 16 to 20	χ^2	df	P
Small	1	a	a	a	b	b	1.517	3	0.68
	2	a	a	b	c	c	0.476	1	0.52
	3	a	b	b	c	c	3.244	2	0.20
Large	1			a	b	c	[1]		
	2	b	a	a	b	b	2.695	3	0.44
	3	a	b	a	c	c	2.892	2	0.24

[1] Zero degrees of freedom.

Table 3

Chi-squared statistics for the constant model of misgraded prawn size in each period of catch (1: July–December 1993, 2: January–June 1994, and 3: July–December 1994), for both small and large packs. $^{*}P< 0.0001$

Period	Small pack	Large pack
1	45.088*	17.963*
2	45.916*	55.701*
3	32.915*	83.060*

Table 4

Chi-squared statistics for the constant model of misgraded prawn size in each size grade for both small and large packs. $^{*}P< 0.0001$, $^{**}P= 0.13$, $^{***}P= 0.03$.

Size grade	Small pack	Large pack
6 to 8	4.1494**	14.408*
9 to 12	33.271*	4.7639***
13 to 15	220.58*	27.039*
16 to 20	16.159*	106.83*

Of the prawns misgraded, 92% were sized either one grade larger or smaller. Of those misgraded in the 16 to 20 grade, 11% were misgraded by as much as two grades, whereas less than 2% were so misgraded for the other size grades.

The misgrading proportions can again be used in Equation 5 to obtain the at-sea grade-size distribution for these large packs. Shown in Table 5 are these corrected distributions compared with at-sea gradings; here the adjustments can be seen to be more substantial than those for the small packs, particularly for the smaller grades 13 to 15 and 16 to 20 prawns per pound, owing to the tendency of the fishermen to classify the prawns to smaller size grades.

Discussion

Our analysis indicates that small prawns are graded less accurately than large ones. Given that the length

Table 5

Size-grade distributions, expressed as proportions, from grading at sea and adjusted according to Equation 5.

Size grade	Period 1 (July–December 1993)		Period 2 (January–June 1994)		Period 3 (July–December 1994)	
	at-sea	adjusted	at-sea	adjusted	at-sea	adjusted
Small packs						
Under 6	0.15	0.14	0.012	0.015	0.098	0.097
6 to 8	0.16	0.17	0.19	0.19	0.11	0.11
9 to 12	0.30	0.33	0.31	0.30	0.32	0.30
13 to 15	0.26	0.23	0.28	0.28	0.24	0.23
16 to 20	0.13	0.11	0.21	0.20	0.24	0.24
Over 20	0	0.015	0	0.014	0	0.018
Large variable packs						
Under 6	—	—	0.11	0.071	0.12	0.15
6 to 8	—	—	0.059	0.11	0.17	0.15
9 to 12	0.079	0.12	0.12	0.16	0.22	0.28
13 to 15	0.055	0.43	0.10	0.22	0.14	0.21
16 to 20	0.87	0.42	0.61	0.38	0.36	0.20
Over 20	0	0.030	0	0.069	0	0.017

range corresponding to the small commercial grades is narrow (Table 1), it is perhaps not surprising that small prawns tend to be misgraded more frequently. Alternatively the grading of small prawns may be less accurate because they are less valuable than large prawns and therefore less time is spent on grading each individual.

In small packs, misgraded prawns were generally graded into larger categories, whereas in large packs, those misgraded were generally placed into smaller categories.

Incorrectly graded prawns from both pack sizes, however, tend to be incorrectly graded by only one size category, so that all prawns were graded to within three and six millimeters carapace length of their corresponding size grade.

The high proportion of landings graded and the accuracy of some of this grading suggest that size information contained in the NPF logbooks could be valuable for stock assessment. Most prawns sold in small (3-kg) packs have been accurately graded by fishermen, and these gradings could be used as a reasonable measure of the length-frequency distribution of the prawns. However, prawns sold in larger (12–15 kg) packs are graded less accurately, especially for the smaller grade sizes, and it is recommended that data from quality inspections be used to correct fishermen's grade-size distribution.

Although the work outlined in this paper was done for the Australian northern prawn fishery, similar analyses using similar methods could be carried out for other fisheries if comparable data on size gradings were available.

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Digestive tract parasites in rhynchoteuthion squid paralarvae, particularly in *Illex argentinus* (Cephalopoda: Ommastrephidae)

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Cephalopods play an important role in the transfer of parasites through the food web. They are second and third intermediate hosts for larval stages of digeneans, cestodes, and nematodes. The final hosts are usually fishes, sea birds, and marine mammals (Hochberg, 1990). Nevertheless, the interactions of cephalopods and their parasites are still poorly understood, and almost nothing is know about parasitism in cephalopod paralarvae and early juveniles (Vecchione, 1987). Information on parasitism in the early stages of cephalopod life cycles can provide a better understanding of host-parasite relationships as well as the environment and conditions in which infection first occurs.

Ommastrephid paralarvae are among the smallest cephalopods at hatching and are termed "rhynchoteuthion" because their tentacles are fused into a proboscis-like structure. Three distinct morphological types of rhynchoteuthion paralarvae (types "A," "B," and "C") are found commonly off southern Brazil (Haimovici et al., 1995). "Type C" is *Illex argentinus* (Castellanos, 1960) and "type A" probably is *Ommastrephes bartramii* (Lesueur, 1821). *Illex argentinus* is distributed in the southwestern Atlantic Ocean from 22° to 54°S (Roper et al., 1984), and it currently supports the largest squid fishery in the world. This species is an important link in the trophic relations of the pelagic ecosystem of this region and constitutes a major element of the diet of several commercial fishes, such as *Thunnus obesus*, *Merluccius hubbsi*, *Xiphias gladius*, and *Polyprion americanus* (Santos, 1992; Ivanovic and Brunetti, 1994).

The digestive tract contents of *Illex argentinus* and the other rhynchoteuthion types were examined by Vidal and Haimovici (1998). During examination of the digestive tracts, observations on parasitism were made. In this note we report the parasites (protistans and metazoans) found in the digestive tract of rhynchoteuthion paralarvae, mainly *Illex argentinus*.

Material and methods

Ommastrephid paralarvae were collected in four surveys carried out between Cape of Santa Marta Grande (28°30'S) and Chuí (34°20'S), Brazil, during the spring of 1987, summer of 1990, autumn of 1991, and winter of 1988. Paired bongo nets, with 60-cm mouth diameter and 0.33-mm mesh were used in oblique tows between the surface and depths of approximately 300 m. This gear was towed at a speed of 2 kn and deployed for 5–15 min. Afterwards, paralarvae were fixed and preserved in formalin.

Digestive tracts were examined from paralarvae of 72 *I. argentinus* (1.0–8.0 mm of mantle length (ML)), 12 "type A" (1.0–5.8 mm ML) and 4 "type B" (2.0–4.0 mm ML). Paralarvae were stained with alcian blue and then cleared with trypsin, following the method of Vecchione (1991). This method makes the paralarvae semitransparent and the parasites in the gut easier to see. The stomach, caecum, and intestine of all paralarvae were examined for parasites with a light microscope at a magnification of 400×. The esophagus was not examined. Five *I. argentinus* juveniles (16.0–38.0 mm ML) and 14 paralarvae (1.6–9.7 mm ML) of *I. argentinus* with no previous clearing and staining treatment were also examined. The prevalence and the mean intensity of infestation (number of a particular parasite per infected individuals) were calculated according to Margolis et al. (1982).

Results

Parasites were not found in the 14 untreated paralarvae. The opaque walls of the internal organs made the visualization of parasites difficult. A single copepod parasite was found in one of the five untreated juveniles.

Four types of parasites were observed in paralarvae and juvenile *I. argentinus*: coccidians (Apicomplexa: Sporozoea: Eucoccidiida), didymozoid-metacercariae (Platyhelminthes: Trematoda: Digenea),

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Table 1

Results of examinations of rhynchoteuthion paralarvae from four surveys conducted between the spring of 1987 and autumn of 1991. + = presence; 0 = absence.

	Spring 1987		Summer 1990	Autumn 1991		Winter 1988
	Illex argentinus	"Type B"	"Type A"	*Illex argentinus*	"Type B"	*Illex argentinus*
Paralarvae mantle length (mm)	1.0–8.0	2.8	1.0–5.8	1.3–5.5	2.0–4.0	1.0–7.8
Digestive tracts examined	41	1	12	19	3	12
Parasites:						
Nematode	+	0	0	0	0	0
Aggregata sp. (coccidian)	0	0	0	0	0	+
Didymozoids						
Monilicaecum sp.	+	0	+	+	0	+
Prevalence (%)	7.3		72.0	10.5		8.3
Mean intensity of infestation	2.3		3.5	1.5		1.0

a nematode (Nematoda) and a copepod (Arthropoda: Crustacea: Siphonostomatoida). About 50 coccidians (*Aggregata* sp.) were found distributed along the caecum wall of a 7.8-mm-ML paralarva collected in winter. Because the paralarva was preserved in glycerin for several months, taxonomic details of the parasites were not very clear. Cyst capsules (sporocystes) varied in size from 11 to 17 µm. However, the detailed structures inside the capsules were obscure and no certainty could be attained about the presence of sporozooites; hence this protozoan was assigned to the genus *Aggregata*. The observed parasites may have been in a very early stage of development and if the capsules actually represent sporocystes they were unusual because only 1 or 2 were present inside an amorphous oocyst mass (Hochberg[1]). These parasites are deposited at the Santa Barbara Museum of Natural History.

Six *I. argentinus* paralarvae (2.2–6.7 mm ML) from autumn, winter, and spring surveys contained 1–3 didymozoid metacercariae, probably type *Monilicaecum*. The body dimensions of the parasites ranged from 140 to 200 µm and because of their size and the absence of testicular anlagen, they appeared to be recently hatched. A single trematode attached to the caecum wall was found in the smallest paralarva. Three parasites were found in the largest paralarva, two attached to the stomach wall and one near the buccal mass. In the other paralarvae, the parasites were found attached to the caecum wall. Data on prevalence and mean intensity of infestation of different paralarval types and surveys of didymozoids are presented in Table 1. We found a single (nematode attached to the caecum wall of a 7.0-mm-ML rhynchoteuthion from the spring sample. The copepod parasite was located on the caecum wall of a 38.0-mm-ML juvenile obtained in spring. The copepod was identified as an adult male of *Metacaligus uruguayensis* (Siphonostomatoida: Caligidae) (Ho and Bashirullah, 1977). *Illex argentinus* is a newly recorded host for *M. uruguayensis*.

In the summer of 1990, didymozoid metacercariae were found in "type A" rhynchoteuthions from 2.0 to 5.0 mm ML. Prevalence was 72% and the mean intensity of infestation was 3.5 (Table 1). All were attached to the caecum or stomach walls, except for three parasites attached to the inner wall of the mantle and two others to the caecum wall of a single paralarva (3.6 mm ML).

Parasites were not found in "type B" rhynchoteuthions. However, only four paralarvae of this type were examined.

Discussion

Illex argentinus first acquire didymozoid metacercariae as small rhynchoteuthions. Hatchlings typically are found off southern Brazil at the outer shelf and slope in tropical and subtropical waters (Vidal and Haimovici, 1997). The infestation may be related to the fact that paralarvae are distributed mainly in tropical waters, where cystophorous cercariae may be abundant and not necessarily because the paralarvae are eating infected intermediate hosts. Crustacean prey were not found in the digestive tracts of rhynchoteuthions smaller than 3.7 mm ML (Vidal and Haimovici, 1998). However, paralarvae larger than this size could also be infested by consuming infected second-intermediate hosts, such as copepods and other crustaceans.

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[1] Hochberg, F. G. 1997. Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Personal commun.

Infestation in the smaller rhynchoteuthions may occur when free cystophorous cercariae are released into the plankton and passively enter the mantle cavity during respiration (Gaevskaya, 1976) or when the cercariae attach to mucus that covers the mantle and head of rhynchoteuthions. They may also be ingested directly, in the same way that crustaceans are infested. If this is true, ommastrephid paralarvae may act as second intermediate hosts for some didymozoids. The presence of didymozoid metacercariae in the digestive tracts of rhynchoteuthions as small as 2.0 mm ML shows that the infection occurs well before that previously recorded by Gaevskaya and Nigmatullin (1983). Additionally, the size of the didymozoid metacercariae type *Monilicaecum* (140–200 µm) found on rhynchoteuthion paralarvae is strong evidence that they are in an early developmental stage in relation to those found on adult *I. argentinus* from southern Brazil (400–800 µm) (Santos, 1992). Our results are in accordance with the suggestion of Hochberg (1990) that didymozoids can grow inside the squid host. Hochberg (1990) also reported that a peak of infestation by didymozoids occurs in squids from 10 to 25 cm in ML. Nevertheless, infection decreases in adult individuals (Gaevskaya and Nigmatullin, 1977, 1983) owing to the fact that the didymozoids die after they reach a maximum size in a specific host (Hochberg, 1990). Larger squids may be reinfected by didymozoid metacercariae when they feed on infested fish prey (Hochberg, 1990). Our results indicate that more paralarvae should be examined in the future. If it is correct to assume that recently hatched didymozoid metacercariae usually infest early paralarvae, information on size and developmental stage of both host and parasites would help to understand their relationship better.

Didymozoid metacercariae were found in *I. argentinus* rhynchoteuthions from autumn to spring and in "type A" rhynchoteuthions during the summer. This morphotype had a higher prevalence and infestation of didymozoids than those of *I. argentinus*. They were collected in the summer of 1990, when tropical waters dominate the study area (Vidal and Haimovici, 1997). Thus, these larval trematodes are present off southern Brazil throughout the year. This finding is in agreement with the occurrence of the high prevalence and intensities of didymozoid metacercariae in juvenile and immature *I. argentinus* from the same area year around (Santos, 1992).

Only the sexual stages of *Aggregata* occur in cephalopods, whereas asexual stages infect the digestive tracts of crustaceans (Hochberg, 1990). *Aggregata* appears to be host-specific only in cephalopods, not in crustaceans, and is a common parasite of *Sepia* and *Octopus* (Hochberg, 1990). Our study is the first to report its presence in *I. argentinus*. This coccidian has not been found in adults of *I. argentinus* collected off southern Brazil (Santos, 1992) or Argentina (Nigmatullin and Shukhgalter, 1990; Sardella et al., 1990). *Martialia hyadesi*, a southern Atlantic oceanic species, and *Todaropsis eblanae* and *Todarodes sagittatus* in waters off Spain are the other ommastrephid squids in which *Aggregata* have been reported (Gaevskaya et al. 1986, Pascual et al. 1996). It is important to stress that infections by *Aggregata* can only be established after paralarvae begin to feed on crustaceans infected with the asexual stages of the parasite. The infected paralarva observed in this study was 7.8 mm ML; however, crustacean prey, mainly copepods, have been found in the gut of *I. argentinus* paralarvae larger than 3.7 mm ML (Vidal and Haimovici, 1998).

Metacaligus uruguayensis was originally described from the gill cavity of *Trichiurus lepturus* from Venezuela (Ho and Bashirullah, 1977). This genus previously has not been reported from cephalopods (see review by Hochberg, 1990). Associations between copepods and cephalopods appear to be primarily commensal and not truly parasitic (Hochberg, 1990). In southern Brazil, small and large adult *T. lepturus* (70–1000 mm TL) occasionally prey on juvenile and adult *I. argentinus* (22–200 mm ML) (Martins, 1992); however, additional information is required to determine whether *I. argentinus* serves as a final or only an accidental host for this copepod.

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Diet of Pacific sleeper shark, *Somniosus pacificus*, in the Gulf of Alaska

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The sleeper shark, *Somniosus pacificus*, ranges from Chile (Crovetto et al., 1992) through southern California (Phillips,1953), British Columbia to the Gulf of Alaska (Bright,1959), the Bering Sea (Wilimovsky,1954), and Japan (Tanaka et al.,1982). It is thought to be a voracious and versatile feeder and its diet has been shown to include young marine mammals, such as harbor seal, *Phoca vitulina* (Bright,1959), and the southern right whale dolphin, *Lissodelphis peronii*, (Crovetto et al.,1992). The purpose of this study is to describe the diet of the sleeper shark in the Gulf of Alaska area.

Methods

Sleeper sharks were collected in the Gulf of Alaska (Fig. 1) between June and August 1996 from the longline vessel *Alaska Leader*, and the bottom-trawl vessels *Vesteraalen* and *American No. 1*. After dissections onboard, each individual stomach was put in a plastic bag and frozen at sea. Tags recording date, location, and length and sex of shark were included in the sample bag. Information on the station, shark total length (TL) (measurements follow Castro, 1983), and dates samples were collected are listed in Table 1. Stomachs were thawed in the laboratory and stomach contents were analyzed. Prey were identified to the lowest taxonomic level possible. Each prey item was weighed and standard length of prey fish was measured. Percent frequency of occurrence and the percentage of the total weight of each prey item were calculated. Octopus beak measurements were made to estimate live wet weights of octopi. According to Robinson and Hartwick (1983), pigment-upper-lateral-wall length (PULWL) has the best correlation coefficient with the live wet weight of the North Pacific giant octopus, *Octopus dofleini*; we therefore used these PULWLs to estimate the live wet weight of the octopus. Live wet weights of *Octopus dofleini* that had been consumed were calculated by using Robinson and Hartwick's (1983) equation:

$$\ln(PULWL(\text{mm})) = 0.274 \ln(weight(\text{kg})) + 2.674. \quad (1)$$

Results

A total of 13 sleeper shark stomachs were analyzed; two were empty, 11 contained food (Tables 1 and 2). The length of the sleeper sharks ranged from 218 cm to 295 cm TL (mean= 264.5 cm; SD=24.9 cm. Arrowtooth flounder, *Atheresthes stomias*, was the most important prey, representing 67% of the total stomach content weight (64% of frequency of occurrence). The size of arrowtooth flounder consumed by sleeper sharks ranged from 38 cm to 65 cm TL, (mean=44.8 cm; SD=8.0 cm). Other prey included a 48-cm walleye pollock, *Theragra chalcogramma* (5.2% by weight), a single 33-cm rockfish, *Sebastes* sp., a 40-cm Pacific salmon, *Oncorhynchus* sp., and a 26-cm flathead sole, *Hippoglossoides elassodon*, as well as three unidentifiable flatfish. *Octopus dofleini* were the most important invertebrate found in the diet of sleeper sharks, representing 5% of the total stomach contents weight and 73% of the frequency of occurrence. The estimated wet weight of *Octopus dofleini* (based on beak measurements) ranged from 5.65 kg to 29.07 kg (mean=18.51 kg; SD=6.58 kg). The PULWL measurements ranged from 23.3 mm to 36.5 mm (mean=31.78 mm; SD= 3.64 mm). Less important invertebrate prey included squids, snails (*Fusitriton* sp.), hermit crabs, and gammarid amphipods. Fish offal (five arrowtooth flounder heads) was found in one sleeper shark stomach. It represented 12% of the total stomach contents weight and had a frequency of occurrence of 9%. No Steller sea lion parts were found in the 13 sleeper shark stomachs examined.

In our study, three specimens were collected from bottom trawls, ten from longline surveys. The weight of stomach contents of the three specimens collected from bottom trawls (sharks no. 4, 12, and 13) were more than 2000 g (4506 g; 2321 g; and 11,782 g, respectively), whereas weight of stomach contents of the specimens collected from long lines were much lower than those collected from the bottom trawls (only three weighed more than 500 g, one weighed more than 3000 g, and the rest weighed less than 50 g). Less food in the stomachs of the sleeper sharks col-

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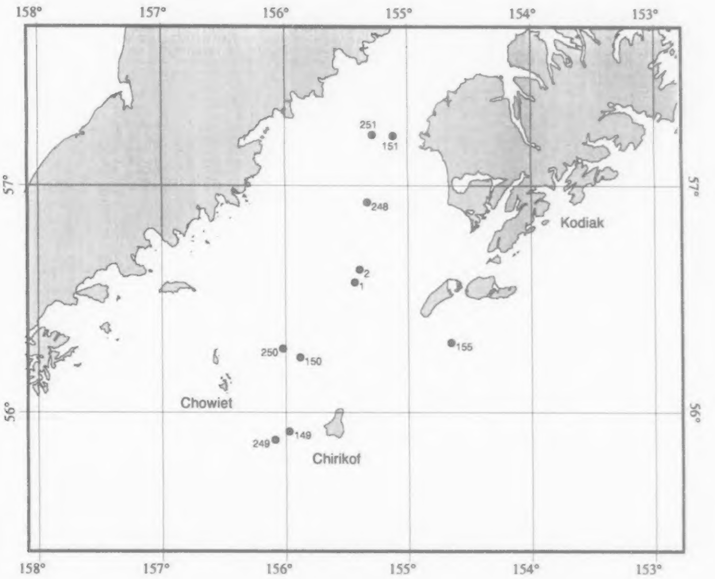

Figure 1

Locations of sleeper sharks collected in Gulf of Alaska

Table 1

Some information on the 13 sleeper shark, *Somniosus pacificus*, stomachs collected in the Gulf of Alaska in 1996. TL = Total length; Wt = stomach contents weight.

Date	Vessel	Station no.	Depth (m)	Shark no.	TL (cm)	Wt (g)
24 Jun '96	*Alaska Leader*	149	241	7	274	520
24 Jun '96	*Alaska Leader*	249	253	11	218	12
25 Jun '96	*Alaska Leader*	250	267	2	292	39
25 Jun '96	*Alaska Leader*	250	267	5	287	3094
25 Jun '96	*Alaska Leader*	250	267	6	249	0
25 Jun '96	*Alaska Leader*	150	240	8	284	821
26 Jun '96	*Alaska Leader*	151	240	1	295	0
26 Jun '96	*Alaska Leader*	151	240	3	274	11
26 Jun '96	*Alaska Leader*	251	255	9	244	11
27 Jun '96	*Alaska Leader*	248	263	10	244	900
28 Jun '96	*Vesteraalen*	155	86	4	274	4506
3 Aug '96	*American No. 1*	1	101	12	229	2321
4 Aug '96	*American No. 1*	2	113	13	274	11,782

lected by longlines is probably caused by regurgitation during the long operation (two to six hours) of longline surveys. Our data also indicate that more prey items (e.g. walleye pollock, salmon, rockfish, and snails) were found in stomachs collected by bottom trawls than collected from longlines (mainly arrowtooth flounder and octopus). Bottom depths (Table 1) for the samples collected from bottom trawls were shallower (from 86 to 113 m) than for samples collected from longlines (from 240 to 267 m); bottom depth may also be a factor in the diet variations. Length of the sleeper sharks (Table 1) might also affect their diet; owing to the small sample size, however, no comparisons could be made from our study.

Discussion

On the basis of our sampling of stomach contents, sleeper sharks appear to feed mainly on the bottom. Even though *Octopus dofleini* represented only 5% of the total stomach content weight, they occurred in a high percentage of sleeper shark stomachs (73%). Other researchers have also found that benthic fish and invertebrates are the predominate species in the diet of sleeper sharks. Phillips (1953) found a sleeper shark in California that had fed on rockfish. Gotshall and Jow (1965) found that the diet of sleeper shark included rex sole, *Glyptocephalus zachirus*; Dover sole, *Microstomus pacificus*; Pacific halibut, *Hippoglossus stenolepis*; and cephalopods.

The diet of sleeper sharks vary with their size. Gotshall and Jow (1965) described the main food of a 114-cm female sleeper shark as *Moroteuthis robusta*. In our study lengths of sleeper sharks ranged between 200 and 300 cm. Their diets consisted mainly of arrowtooth flounder, walleye pollock, and cephalopods. Larger sleeper sharks (360–400 cm) have been reported to consume not only fishes and cephalopods, but also marine mammals, i.e. harbor seal (Bright, 1959) and southern right whale (Crovetto et al., 1992).

We would like to note that stomach samples used in our study were from the area southwest of Kodiak Island, close to Steller sea lion (*Eumetopias jubatus*) rookeries at Chowiet and Chirikof Islands, as well as near numerous sea lion haulouts (Sease et al., 1993; NMFS, 1995). However, sleeper shark attacks on pups have not been reported at any time of year and we did not find evidence of predation on sea lions in our study. We did find fish offal (five arrowtooth flounder heads) in stomach samples. Bigelow and Schroeder (1948) also reported that Greenland shark, *Somniosus microcephalus* (a similar congeneric species of sleeper shark in the Atlantic Ocean), devours carrion, such as whale meat and blubber from whaling operations. It seems that sleeper shark, like Greenland shark, is sluggish and likes to stay on the bottom, feeding opportunistically on what they encounter in the environment (including carrion and fish offal).

Table 2

Prey items (expressed in percent frequency of occurrence (%FO), and percent total weight (%W)) of sleeper shark, *Somniosus pacificus*, collected in Gulf of Alaska in 1996.

Prey name	%FO	%W
Gastropod (snail)	9.09	0.49
Fusitriton sp. (snail)	9.09	0.19
Cephalopod (squid and octopus)	27.27	0.17
Teuthoidea (squid)	36.36	0.62
Octopus dofleini (octopus)	72.73	4.63
Crangonidae (shrimp)	9.09	0.01
Pagurid (hermit crab)	9.09	0.01
Teleostei (unidentified fish)	45.45	0.33
Oncorhynchus sp. (salmon)	9.09	4.49
Gadidae (gadid fish)	9.09	0.49
Theragra chalcogramma (walleye pollock)	9.09	5.22
Atheresthes stomias (arrowtooth flounder)	63.64	67.21
Sebastes sp. (rockfish)	9.09	2.06
Pleuronectid (unknown flatfish)	18.18	0.86
Hippoglossoides elassodon (flathead sole)	9.09	0.98
Fishery offal	9.09	12.27
Total prey weight (g)	24,017	
Number of stomachs with food	11	
Number of empty stomachs	2	

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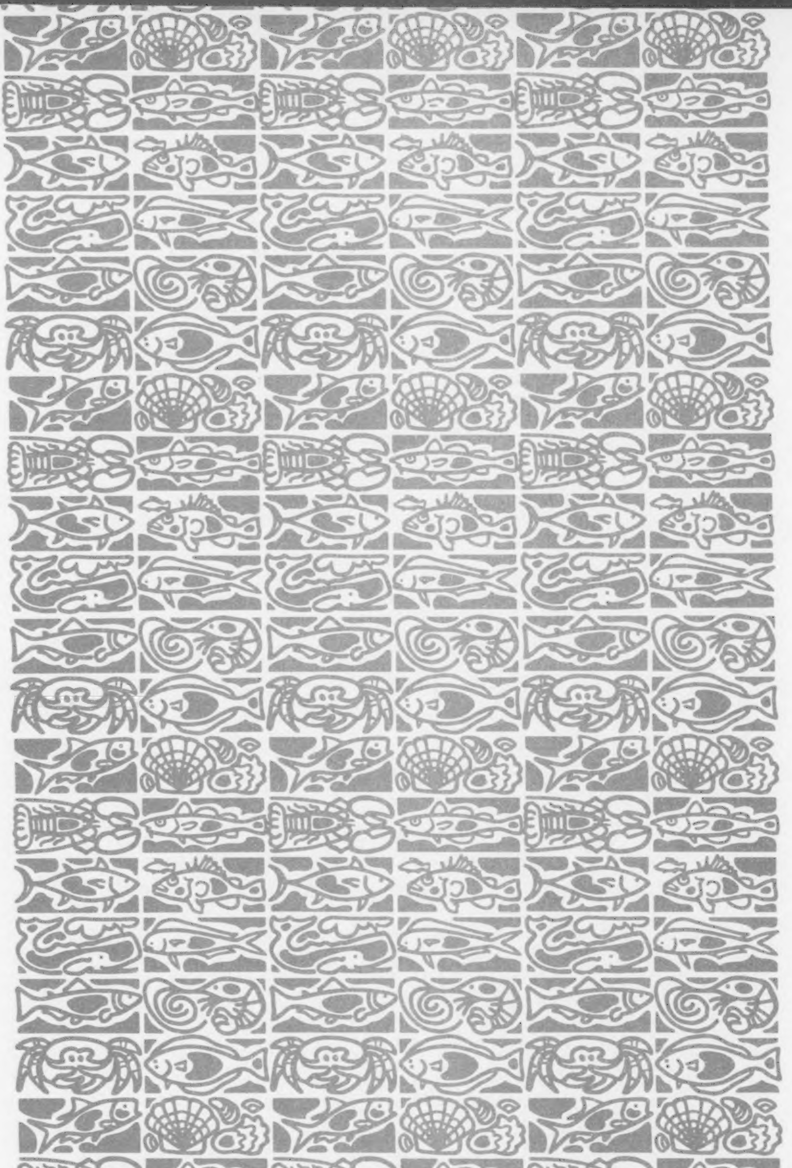☆ U.S Gov. Printing Office 1999
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